Hind limb proportions and kinematics: are small primates different from other small mammals?

Manuela Schmidt

Institut für Spezielle Zoologie und Evolutionsbiologie, Friedrich Schiller Universität Jena, Erbertstrasse 1, D-07743 Jena, Germany

e-mail: schmidt.manuela@uni-jena.de

Summary

Similar in body size, locomotor behaviour and morphology to the last common ancestor of Primates, living small quadrupedal primates provide a convenient model for investigating the evolution of primate locomotion. In this study, the hind limb kinematics of quadrupedal walking in mouse lemurs, brown lemurs, cotton-top tamarins and squirrel monkeys are analysed using cineradiography. The scaling of hind limb length to body size and the intralimb proportions of the three-segmented hind limb are taken into consideration when kinematic similarities and differences are discussed.

Hind limb kinematics of arboreal quadrupedal primates, ranging in size between 100 g and 3000 g, are size independent and resemble the hind limb kinematics of small non-cursorial mammals. A common feature seen in smaller mammals, in general, is the horizontal position of the thigh at touchdown and of the lower leg at lift-off. Thus, the maximum bone length is immediately transferred into the step length. The vertical position of the leg at the beginning of a step cycle and of the thigh at lift-off contributes the same distance to pivot height. Step length and pivot height increase proportionally with hind limb length, because intralimb proportions of the hind limb remain fairly constant. Therefore, the strong positive allometric scaling of the hind limb in arboreal quadrupedal primates affects neither the kinematics of hind limb segments nor the total angular excursion of the limb. The angular excursion of the hind limb in quadrupedal primates is equal to that of other non-cursorial mammals. Hence, hind limb excursion in larger cercopithecine primates differs from that of other large mammals due to the decreasing angular excursion as part of convergent cursorial adaptations in several phylogenetic lineages of mammals. Typical members of those phylogenetic groups are traditionally used in comparison with typical primates, and therefore the 'uniqueness' of primate locomotor characteristics is often overrated.

Key words: joint kinematics, angular excursion, intralimb proportions, limb length scaling, *Microcebus murinus*, *Eulemur fulvus*, *Saguinus oedipus*, *Saimiri sciureus*.

Introduction

Primate quadrupedalism is said to be different from that of other placental mammals in a number of ways. Absolute characteristics include grasping hind feet combined with a diagonal-sequence gait during arboreal quadrupedalism (Hildebrand, 1967; Cartmill et al., 2002; Lemelin et al., 2003), a posterior weight shift (Kimura et al., 1979; Reynolds, 1985) and a humeral protraction over 90° relative to the horizontal plane (Larson et al., 2000).

These characteristics are generally present in arboreal quadrupedal primates and are absent even in the nearest relatives of primates as well as in the majority of other placental mammals. Deviations occur only in primates with more specialised locomotor habits such as slow climbing loris and pottos (Ishida et al., 1990; Schmitt and Lemelin, 2004) and terrestrial quadrupedal cercopithecines (Vilensky and Larson, 1989; Demes et al., 1994). Thus, grasping hind feet, the diagonal-sequence gait, the posterior weight shift and a large humeral protraction are hypothesised to be 'unique' to the Order Primates, representing a suite of derived characteristics. The convergent evolution of such characteristics in several arboreal marsupials may imply functional relationships between some or all of these characteristics (Rasmussen, 1990; Schmitt and Lemelin, 2002; Lemelin et al., 2003).

Other characteristics proposed as 'unique' to primates are larger step lengths (Alexander and Maloiy, 1984; Reynolds, 1987), greater angular excursions of the fore and hind limbs (Reynolds, 1987; Larson et al., 2000, 2001), greater long bone lengths (Alexander et al., 1979) and a more compliant walk in comparison with other mammals (Schmitt, 1999). However, based on a broad sample of mammalian species belonging to different phylogenetic groups, Larney and Larson (2004) found that limb compliance does not appear to be exclusive to primates. Obviously, whether such relative features are hypothesised to be primate-specific characteristics or not

depends on the criteria for the sample selection and the extent to which the comparative method is applied.

In most investigations of primate locomotor characteristics, special emphasis is devoted to the differences between typical primates and typical non-primates (Kimura et al., 1979; Alexander and Maloiy, 1984; Reynolds, 1987; Schmitt, 1999). Typical primates are mostly Old World cercopithecine monkeys, apes and New World atelines. The artificial group 'non-primate mammals' is generally defined as domestic animals such as carnivores, ungulates and rodents because kinematic data can be easily gathered for these animals. The proposed uniqueness of primates with regard to step length, limb angular excursion, and long bone lengths is therefore based on comparison between such 'typical' representatives of different phylogenetic groups. Only Larson et al. (2000, 2001) support their conclusions on a broad sample of mammalian species, but they concentrate their attention on the pronounced differences between the larger animals of their sample group, instead of examining the similarities among smaller species.

Primates and other mammalian groups diverge with increasing body size with respect to hind limb excursion angle, whereas differences seem less pronounced in small members (below 5 kg) of all groups (Larson et al., 2001). Yet Larson et al. (2001) confirm the previous findings of Reynolds (1987) that primates have a greater hind limb angular excursion than other mammals. The question is: how can one decide if hind limb excursion has increased during primate locomotor evolution or if hind limb excursion has decreased in the other groups due to convergent cursorial adaptations in those lineages? Observed differences among primates and the phylogenetically distinct living carnivores, rodents, artiodactyls and perissodactyls have amassed a host of evolutionary changes along at least five phylogenetic lineages. The assertion that the primate order is characterized by a derived limb excursion pattern requires a clearer demonstration of character polarity for this feature in primates and their sister taxa. Hence, smaller primates possessing postcranial character states more similar to those preserved in the fossil record may offer better insights about locomotor evolution than the typically studied, highly derived cursorial forms.

Most extant orders of placental mammals appeared in the fossil record over a relatively short period of time, ranging between 50 and 70 million years ago, hence interordinal relationships are far from resolved. Nevertheless, the adaptive nature of the last common ancestor of placental and marsupial mammals appears to reflect a non-cursorial locomotor mode adapted for moving on uneven, disordered substrates (Jenkins, 1971; Fischer, 1994). Jenkins (1974), based on his study of habitat-related behaviour and locomotor performance in tree-shrews, proposed that the distinction between 'arboreal' and 'terrestrial' locomotion is artificial for tiny forest-dwellers such as tree-shrews because most substrates in the forest require the same basic locomotor repertoire. More recently, Fischer et al. (2002) have demonstrated that small mammals, independent of their phylogenetic position or natural habitat type, generally display similar overall kinematic aspects of limb displacement during locomotion.

The phylogenetic origin of the Order Primates within placental mammals is still being discussed, and the sister-group of the Primates remains contentious. Proposed extant sister groups of primates include the small quadrupedal tree shrews (Wible and Covert, 1987) and the gliding Dermoptera (Cronin and Sarich, 1980; Beard, 1993). Despite the lack of consensus on the actual sister taxon of primates, tree shrews have been considered a reasonable morphological model for the last common ancestor of primates and their closest relatives.

Although not all living primates are tree-dwellers, they all appear to derive from arboreal small-bodied ancestors (Cartmill, 1972; Gebo, 2004). Unlike tree-shrews, primates possess an opposable nailed hallux responsible for the grasping capabilities of the hind feet. The hallux of tree-shrews is able to abduct but not to oppose against the other digits (Jenkins, 1974). Supported by the coincidence of small body size and grasping hind feet, small terminal branches in the top of the trees are suggested to be the locomotor habitat of the last common ancestor of living primates (Cartmill, 1972, 1974).

The aim of this study is to compare the hind limb kinematics of a selection of small arboreal quadrupedal primates with those of tree-shrews and other small mammals that exhibit an unspecialised locomotor behaviour comparable with the ancestral mode of mammalian locomotion. In this way, ancestral and derived primate-specific characteristics of hind limb kinematics can be differentiated. Scaling of hind limb length to body size and the intralimb proportions of the three-segmented hind limb are also considered in relation to the similarities and differences in hind limb kinematics.

Materials and methods

Animals

Hind limb kinematics were compared in two individuals of each of four species of primarily arboreal quadrupedal primates: grey mouse lemur (Cheirogaleidae; *Microcebus murinus* J. F. Miller 1777), brown lemur (Lemuridae; *Eulemur fulvus* E. Geoffroy St Hilaire 1796), cotton-top tamarin (Callitrichidae; *Saguinus oedipus* Linnaeus 1758) and squirrel monkey (Cebidae; *Saimiri sciureus* Linnaeus 1758). The body mass, sex and age of the animals are recorded in Table 1. The animals were kept in accordance with German animal welfare regulations, and experiments were registered by the Committee for Animal Research of the Freistaat Thüringen, Germany.

Mouse lemurs are the smallest primates in the world. They are found only in Madagascar and inhabit the dense leafy areas of the secondary forest with tangles of fine branches and lianas (Martin, 1973). Mouse lemurs are agile and active at night, usually travelling along branches on all four legs.

The family Lemuridae is also confined to Madagascar. Members of the genus *Eulemur* are arboreal forest-dwellers. The brown lemur is by far the most widespread of the 'typical' lemurs and is divided into no less than six subspecies. Lemurs are active, quadrupedal animals that run and walk on horizontal

Table 1. *Body mass, sex and age of the animals used for the kinematic analysis*

Individuals	Body mass (g)	Sex	Age (years)
Microcebus murinus	90	Male	2
Microcebus murinus	110	Male	3
Eulemur fulvus	3000	Male	>20
Eulemur fulvus	2100	Female	10
Saguinus oedipus	450	Male	10
Saguinus oedipus	520	Female	17
Saimiri sciureus	1100	Male	6
Saimiri sciureus	850	Male	3

and oblique branches and are capable of leaping to and from vertical and horizontal supports (Garbutt, 1999).

Members of the family Callitrichidae are among the smallest of primates. They are found in the tropical forests of Central and South America, mainly in the Amazon region. The thumb of tamarins and marmosets is not opposable, and all the digits bear pointed, sickle-shaped nails, except the great toe, which has a flat nail. Callitrichids are sometimes considered primitive, squirrel-like primates. Most tamarins (*Saguinus*, *Leontopithecus*, *Callimico*) are active arborealists that move by running quadrupedally along thin horizontal branches and leaping between terminal supports (Fleagle and Mittermeier, 1980; Garber, 1980; Sussmann and Kinzey, 1984). Unlike tamarins, marmosets (*Callithrix*) forage on large vertical supports rather than on small flexible branches (Cartmill, 1974; Hershkovitz, 1977).

Squirrel monkeys are among the small members of the family Cebidae. Squirrel monkeys are found in primary and secondary forests of Central and South America, where they are commonly found in the lower levels. They are arboreal quadrupeds that frequently leap (Thorington, 1968).

Motion analysis

Each of the individuals was trained to walk on a raised pole or on a horizontal motor-driven rope-mill, an arboreal analogue of a treadmill. The diameter of the support was adapted to the preferred natural substrate of the species (mouse lemur, 10 mm; cotton-top tamarin, 25 mm; squirrel monkey, 30 mm; brown lemur, 50 mm). Data on substrate preferences were obtained from several sources (Tattersall, 1977; Walker, 1974; Garber, 1980; Gebo, 1987; Arms et al., 2002). Rope-mill speed was not fixed but adjusted to obtain the animal's preferred walking speed.

Uniplanar cineradiographs were collected in lateral view at 150 frames s^{-1}, in order to visualize joints and obtain angular excursions of limb segments. Segment abduction angles were approximated from the foreshortening of the bones in the parasagittal projection. The methods of collecting and processing kinematic variables from cineradiographs have been described elsewhere in detail (Schmidt and Fischer, 2000; Schmidt, 2005) and will be summarised only briefly here. The x-ray equipment consists of an automatic Phillips® unit with

one x-ray source that applies pulsed x-ray shots (Institut für den Wissenschaftlichen Film, Göttingen, Germany). Distortions of the x-ray maps were corrected by reference to an orthogonal grid of steel balls (diameter 1.0 mm, with a mesh width of 10.0 mm), filmed before and after each experimental session. The x-ray images were recorded from the image amplifier either onto 35 mm film (Arritechno R35-150 camera) or using a high-speed CCD camera (Mikromak® Camsys; Mikromak Service K. Brinkmann, Berlin, Germany). X-ray films were then copied onto video tapes and A/D-converted using a video processing board. Afterwards, these films were analyzed frame-by-frame to identify previously defined skeletal landmarks (software 'Unimark' by R. Voss, Tübingen, Germany; Fig. 1A). The software Unimark calculates angles and distances based on *x*- and *y*-coordinates of the landmarks, correcting the distortions of the x-ray maps automatically with reference to the *x*- and *y*-coordinates of the grid.

The complete dataset obtained for individuals of the four primate species in this study includes approximately 15 000 x-ray frames, with at least 25 steps analyzed for each species.

The following kinematic variables were measured or calculated.

1. Segment angles – calculated relative to the horizontal plane (the term protraction is used for the cranial displacement of the distal end of each segment; retraction describes its caudal displacement) (Fig. 1B).

2. Limb joint angles – defined anatomically and measured at the flexor side of each joint (Fig. 1B).

3. Maximum amplitudes of joint excursions during the support phase – difference between maximum extension angle and maximum flexion angle.
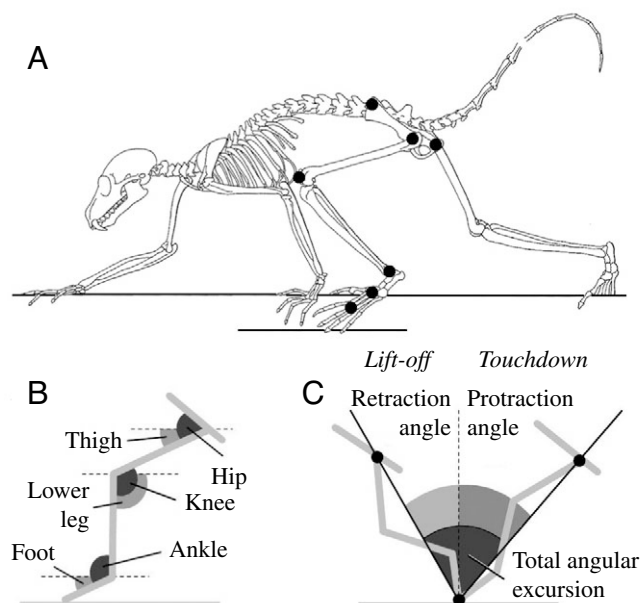

Fig. 1. Motion analysis: (A) skeletal landmarks on the hind limb (illustrated on the brown lemur, *Eulemur fulvus*); (B) calculated joint and segment angles and (C) calculated excursion angles of the hind limb.

Table 2. *Morphometry: specimens, body mass and limb segment lengths*

Specimen	Body mass (g)	Maximum articular length (mm)		
		Femur	Tibia	Tarsometatarsus
Primates				
Cheirogaleidae				
Cheirogaleus major	283	60	58	32
Microcebus murinus	100*	30	33	14
Microcebus murinus	110	33	34	21
Microcebus murinus	90	27	32	13
Microcebus murinus	70	27	30	16
Microcebus myoxinus	31	19	24	12
Microcebus rufus	70*	30	33	19
Microcebus rufus	70*	29	32	18
Microcebus rufus	50	27	31	19
Lemuridae				
Eulemur coronatus	1530	104	101	51
Eulemur fulvus	2145	119	116	52
Eulemur fulvus	2100*	121	113	54
Eulemur fulvus fulvus	3500	132	124	66
Eulemur fulvus fulvus	2500	126	120	66
Eulemur fulvus collaris	2250	124	115	55
Eulemur fulvus collaris	2110	125	117	56
Eulemur fulvus albifrons	2250	123	115	50
Eulemur macaco	2400*	126	113	60
Eulemur mongoz	1250	102	96	54
Lemur catta	2000*	133	129	67
Varecia variegata	3520	126	123	67
Varecia variegata	3470	114	113	62
Varecia variegata	3550*	145	130	79
Varecia variegata	3550*	146	130	79
Galagonidae				
Otolemur crassicaudatus	1100*	89	85	60
Otolemur crassicaudatus	1122	94	83	55
Otolemur crassicaudatus	1050	91	81	53
Otolemur crassicaudatus	900*	78	72	53
Otolemur garnetti	725	88	81	58
Callitrichidae				
Callithrix jacchus	230	59	60	39
Callithrix jacchus	240	59	59	35
Cebuella pygmaea	96	31	33	20
Leontopithecus rosalia	550	62	67	47
Saguinus midas	450	65	62	37
Saguinus oedipus	410	55	61	42
Saguinus oedipus	430	58	60	42
Saguinus oedipus	339	67	68	45
Cebidae				
Aotus nigriceps	780*	91	88	49
Aotus nigriceps	825	89	86	49
Aotus trivirgatus	800*	96	90	52
Cacajao calvus	2800*	132	120	88
Cacajao calvus	3450	159	135	77
Cacajao melanocephalus	2800	152	135	76
Cacajao melanocephalus	3000*	151	133	78
Cacajao melanocephalus	3000*	156	139	79
Callicebus moloch	800*	100	89	47
Callicebus moloch	800*	92	82	49
Cebus apella	1370	128	120	62

Table 2. *Continued*

Specimen	Body mass (g)	Maximum articular length (mm)		
		Femur	Tibia	Tarsometatarsus
Cebidae				
Cebus apella	2000*	132	113	64
Cebus apella	2500*	136	119	65
Cebus capucinus	1300*	118	114	69
Pithecia irrorata	2000*	139	121	63
Pithecia irrorata	2300*	145	127	65
Pithecia irrorata	2200*	142	131	66
Pithecia irrorata	2500*	145	129	65
Pithecia monachus	1500*	91	90	60
Pithecia pithecia	1000*	129	131	73
Saimiri sciureus	708	79	82	52
Saimiri sciureus	800*	84	81	52
Saimiri sciureus	580	78	80	44
Cercopithecidae				
Cercopithecus diana	5000*	171	160	81
Cercopithecus mona	2750	128	125	68
Chlorocebus aethiops	3050	129	133	80
Chlorocebus aethiops	3100	120	121	79
Chlorocebus aethiops	2500	91	90	59
Chlorocebus aethiops	5500	155	140	75
Erythrocebus patas	3400	149	159	93
Erythrocebus patas	4900	163	167	105
Erythrocebus patas	3000*	145	155	83
Lophocebus albigena	5600*	169	160	86
Lophocebus albigena	7000*	206	184	89
Macaca mulatta	5000*	163	150	92
Macaca mulatta	4400	146	141	88
Macaca mulatta	9000*	174	161	102
Macaca nemestrina	14500*	211	187	107
Macaca nigra	4500*	158	143	88
Macaca sylvanus	2150	94	92	69
Papio hamadryas	22790	213	198	127
Papio hamadryas	16750	212	201	126
Papio hamadryas	23500	227	214	131
Papio hamadryas	12000*	237	217	126
Papio hamadryas	12000*	226	208	118
Theropithecus gelada	12000*	174	183	106
Theropithecus gelada	20400	203	217	127
Scandentia				
Tupaia glis	200	38	40	29
Tupaia glis	200	37	41	30
Tupaia glis	200	38	41	31
Tupaia glis belangeri	200	38	39	27
Tupaia glis belangeri	200	37	37	25
Tupaia minor	80	29	30	20
Tupaia tana	230	45	47	31
Marsupialia				
Chironectes minimus	400*	48	50	25
Dasyuroides byrnei	158	31	39	26
Didelphis virginiana	4270	83	78	35
Didelphis virginiana	2200	85	84	34
Isoodon obesulus	600*	47	47	25
Marmosa robinsoni	86	25	27	11
Marmosa robinsoni	80	25	28	11
Monodelphis domestica	77	27	27	13

Table 2. *Continued*

Specimen	Body mass (g)	Maximum articular length (mm)		
		Femur	Tibia	Tarsometatarsus
Marsupialia				
Philander opossum	800*	54	60	25
Trichosurus vulpecula	2500*	83	81	35
Trichosurus vulpecula	2500*	85	82	35
Trichosurus vulpecula	3500*	98	94	45
Rodentia				
Atlantoxerus getulus	350	42	33	14
Cynomys ludovicianus	900*	40	40	26
Galea musteloides	360	38	45	29
Galea musteloides	400	38	44	30
Rattus norvegicus	350	34	41	31
Ratufa indica	1500*	78	79	52
Sciurus carolinensis	550	55	62	38
Sciurus vulgaris	400*	56	61	38
Sciurus vulgaris	300*	53	58	35
Sciurus vulgaris	300*	52	57	34
Spermophilus citellus	200*	34	35	21
Spermophilus lateralis	250	38	39	24
Spermophilus lateralis	250	38	39	23
Tamias sibiricus	108	39	33	22
Carnivora				
Canis lupus	38000*	229	225	158
Felis catus	5000*	130	141	94
Mustela putorius	1200	56	56	36
Mustela putorius	800	47	47	32
Mustela putorius	700	47	46	31
Potos flavus	2000*	90	88	56
Potos flavus	1820	80	74	44
Procyon lotor	6800	117	121	64
Vulpes vulpes	4900	123	136	88
Vulpes vulpes	6300	135	143	93

*The asterisk denotes that body mass is compiled from one of the following sources: Grzimek (1987), Rowe (1996), Nowak (1999).

4. Total angular excursions of the hind limb – measured as the angle between the lines connecting the point of ground contact and the proximal pivot at touchdown and lift-off (Fig. 1C).

5. Protraction angle and retraction angle of the hind limb – total angular excursion was divided into an anterior and a posterior angle by drawing a vertical line through the point of ground contact (Fig. 1C).

6. Relation between anatomical limb length and the shortest functional limb length (distance between the proximal pivot and the point of ground contact) at midsupport, which is the vertical alignment of ground contact and the proximal pivot of the limb.

Morphometry

Skeletal specimens (*N*=118) belonging to 58 mammalian species were examined at the Phylogenetisches Museum, Jena and at the Museum für Naturkunde, Berlin, Germany. Adult status of the specimens was judged by fusion of the epiphyses of the long bones. Table 2 lists the different specimens analyzed in this study and indicates the body mass values. Those specimens labelled with an asterisk denote specimens for which body masses were compiled from the literature (Grzimek, 1987; Rowe, 1996; Nowak, 1999). All other body mass values were associated with actual specimens.

The majority of taxa included in the primate sample consist of arboreal quadrupedal primates. Included members of the Cheirogaleidae, Lemuridae, Galagonidae, Callitrichidae and Cebidae prefer to walk and run quadrupedally along narrow branches but also use other modes of progression such as climbing and leaping. However, none of these named taxa shows distinct specialisations for climbing or leaping (e.g. extremely elongated hind limbs; Grzimek, 1987; Rowe, 1996; Fleagle, 1999; Nowak, 1999). Only cercopithecine Old World monkeys (baboons, macaques, patas monkeys, guenons) are basically adapted to terrestrial quadrupedalism (McCrossin et al., 1998; Fleagle, 1999). Still, most guenons and some macaques have returned to arboreality. Hence, re-adaptations to

arboreality in these animals were observed to affect the kinematics and morphology of the autopodia rather than that of proximal limb joints (Meldrum, 1991; Schmitt and Larson, 1995). Unlike strepsirhine and platyrrhine arboreal quadrupeds, the limbs of tree-dwelling cercopithecines are rather extended and adducted, moving primarily in a parasagittal plane (Meldrum, 1991; Schmitt, 1999). The samples of rodents, carnivores and marsupials include both arboreal and terrestrial quadrupeds. Still, cursorial adaptations to terrestrial running occur only in some of the Carnivora (grey wolf, red fox, domestic cat; Jenkins and Camazine, 1977; Nowak, 1999).

Table 2 also contains the measured values of the lengths of the three functional hind limb segments (femur, tibia and tarsometatarsus) for each specimen. The calculation of average values for each species was rejected because there is no evidence that bone length scales isometrically with body size among different sized conspecifics. Rather, an intraspecific allometric scaling is more likely because long bones scale differentially with body size ontogenetically (Jungers and Fleagle, 1980; Roth, 1984; Turnquist and Wells, 1994; Lammers and German, 2002; N. Schilling and A. Petrovitch, manuscript submitted) and across taxa (Aiello, 1981; Jungers, 1985; Bertram and Biewener, 1990; Christiansen, 1999; Lilje et al., 2003). Hind limb length is calculated as the sum of the lengths of the three segments. Body mass is employed as the most appropriate and meaningful size variable for the scaling analysis of hind limb length (Aiello, 1981; Jungers, 1985).

The data were transformed to logarithms to normalize the distribution of the dependent variable Y, and linear regression lines were fitted to the data by means of the reduced major axis model (model II). The reduced major axis model was used rather than least-square regression because the latter assumes that there is no error term associated with the X variable (body mass) (Sokal and Rohlf, 1995). As the body mass of most specimens included here was taken as an average from the literature, it can hardly be considered free of statistical error. Furthermore, the use of least-square regression can lead to biased results if log–log bivariate regressions are used (Zar, 1968). Pearson's product-moment correlation coefficient was computed for each taxonomic group, and the 95% confidence interval surrounding the allometry coefficients (slope) of each sample was calculated. If the confidence interval of a slope does not include the value for geometric similarity (0.33), the slope is said to describe significant allometry.

Standard anthropometric indices, traditionally constructed to assess relative limb proportions in mammals, consider the two long bones of the limbs only (crural index = tibia length/femur length×100). Therefore, they are insufficient to assess intralimb proportions of a three-segmented limb. Thus, intralimb proportions in this study are expressed as percentages of each segment length to the sum of the lengths of the three segments.

Results

The hind limb kinematics were compared in four species of primarily arboreal quadrupedal primates: the mouse lemur

(*Microcebus murinus*; Cheirogaleidae), the brown lemur (*Eulemur fulvus*; Lemuridae), the cotton-top tamarin (*Saguinus oedipus*; Callitrichidae) and the squirrel monkey (*Saimiri sciureus*; Cebidae). Some aspects of these data have been previously published in other contexts (mouse lemur in Fischer et al., 2002; squirrel monkey in Schmidt, 2005). The goal of the present study was to examine a sample of small arboreal taxa, including species with postcranial morphologies resembling the ancestral condition for the Order Primates, seeking similarities to and differences from the closely related tree-shrews and to the basic pattern of mammalian locomotion (Jenkins, 1971; Fischer et al., 2002).

For descriptive and comparative convenience, the analysis of limb kinematics focuses on limb configurations at the instant of touchdown and lift-off during a step cycle. Touchdown and lift-off mark the natural subdivision of a step cycle into a support phase and a swing phase. These points can be compared among quadrupedal animals independent of their limb proportions and other peculiarities of their locomotor apparatus.

When interpreting the similarities and differences in hind limb kinematics within primates and between primates and other mammals, it is necessary to consider the influence of body mass and phylogeny upon hind limb length and intralimb proportions. Therefore, a morphometric analysis of these characteristics in a broader sample of quadrupedal primate and non-primate species is included.

Comparison of hind limb kinematics
Angular excursion of the hind limb

Total angular excursion was measured as the angle between the lines connecting the point of ground contact and the proximal pivot at touchdown and lift-off. By drawing a vertical line through the point of ground contact, the total angular excursion can be split into a retraction angle and a protraction angle.

Total angular excursion of the hind limb varies little among the four primate species. It ranges from 74° in the brown lemur to 77° in the cotton-top tamarin at the preferred moderate walking speeds of the animals. Hind limb angular excursion is greater at a slow walking speed. The maximum values at slow steps are 88° in the mouse lemur, 86° in the brown lemur, 87° in the tamarin and 80° in the squirrel monkey.

The protraction angle and retraction angle of the hind limb are nearly equal in the mouse lemur and the squirrel monkey, where the protraction angle exceeds the retraction angle by a maximum of 3°. In the brown lemur and the cotton-top tamarin, the retraction angle is distinctly greater than the protraction angle. Maximum differences of ~8° were observed in the brown lemur.

Kinematics of hind limb segments

The kinematic behaviour of the hind limb segments varies more strongly among the four species than might be expected from their similarity in total limb angular excursion (Fig. 2).

The step cycle begins with a protracted hind limb at

touchdown. The thigh is more or less horizontally positioned – a simple kinematic solution to transmit bone length directly into step length. In the mouse lemur and the brown lemur, the horizontal placement of the thigh is fairly accurate. In some cases, the distal end of the thigh is raised above the hip joint level in these species and also in the cotton-top tamarin (Table 3). In the squirrel monkey, the thigh position at touchdown is more oblique, with the knee joint depressed below the level of the hip joint.

The lesser protracted thigh in the squirrel monkey is compensated for by a greater protraction of the leg at touchdown. The touchdown angle of the leg exceeds 90°, and the ankle is consistently placed in front of the knee joint. Due to this compensation, the protraction angle of the hind limb is

as great as that of the mouse lemur and even greater than those of the cotton top tamarin and the brown lemur. The leg is vertically positioned at the beginning of a step cycle in the mouse lemur, the brown lemur and the tamarin.

All four species place their feet in a semiplantigrade posture and in a manner in which the tarsometatarsus is always displaced parallel to the thigh (Fig. 2). Support contact is made by the metatarsus and phalanges, but the tarsus never touches the support. In the course of the support phase, the metatarsus is also lifted from the ground. The touchdown angle of the tarsometatarsus is quite similar in all four species.

At the end of the stance phase, the femoral shaft is either vertically positioned (mouse lemur, squirrel monkey) or has moved beyond the vertical position (brown lemur, cotton-top
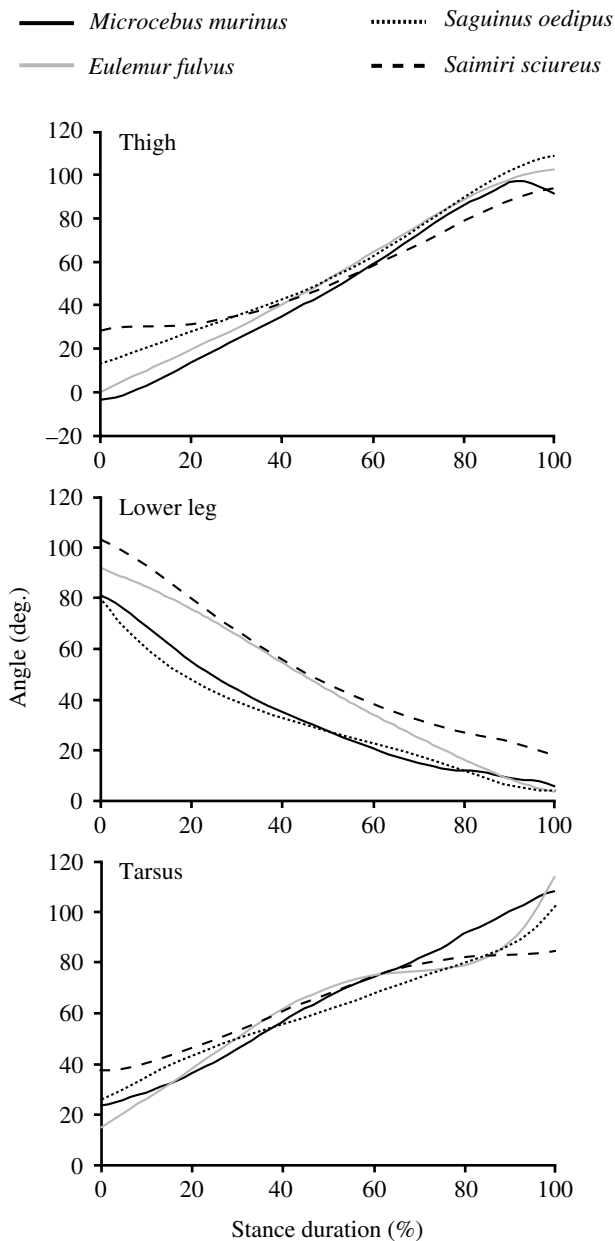

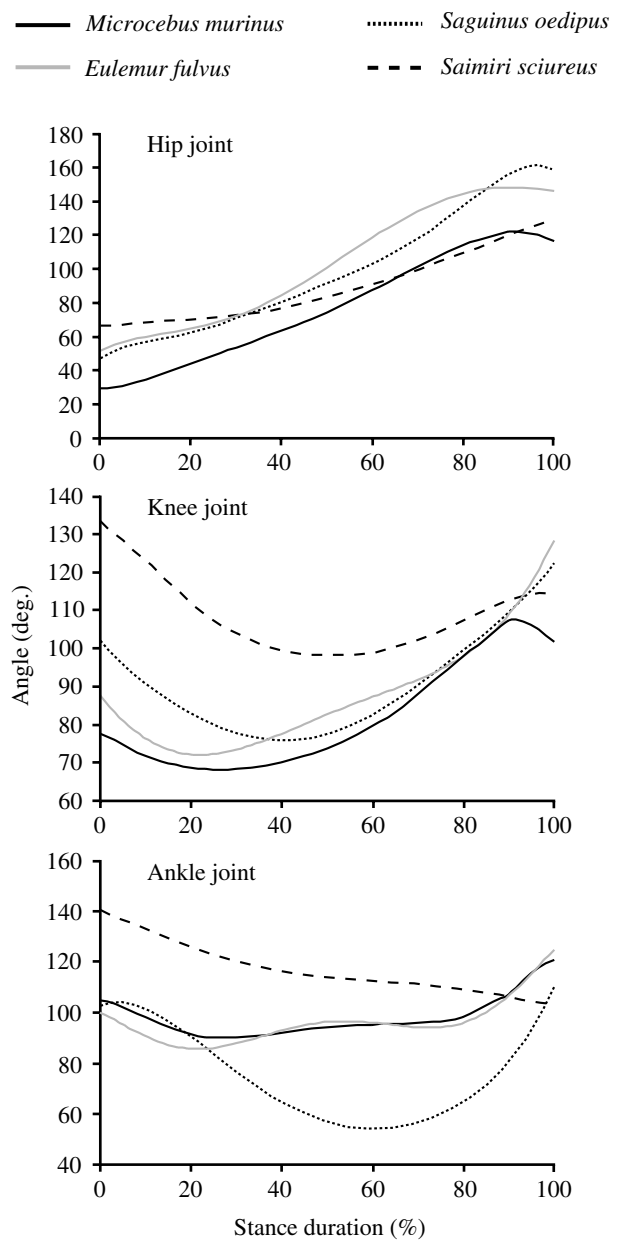Fig. 2. Hind limb segment angles during the support phase of the limb.

Fig. 3. Hind limb joint angles during the support phase of the limb.

tamarin), so that the knee joint is behind the hip joint. The extensive thigh retraction in the brown lemur and the cotton-top tamarin is the main reason for the great retraction angle of the hind limb measured in these two species.

At lift-off, the leg of the lemurs and the tamarin is horizontally positioned or nearly so. In the squirrel monkey, it is rather inclined (Fig. 2). Despite this reduced segment retraction angle, the total excursion angle of the leg is the greatest in the squirrel monkey due to the greater degree of protraction (Table 3). Lower leg kinematics are fairly uniform in the mouse lemur and the brown lemur as well as in the cotton-top tamarin.

Mouse lemurs and brown lemurs retract their tarsometatarsus to a greater degree than do the two New World primates. The segment moves beyond the vertical position in the prosimian species, whereas its retraction ends in a vertical position in the tamarin and the squirrel monkey.

Hind limb excursions outside a parasagittal plane are restricted to the initial phase of propulsion, when the femur is abducted, and adduction of the lower leg brings the foot below the animal's trunk to grasp the pole. Femoral abduction varies between 10° in the squirrel monkey, 22° in the cotton-top tamarin and 38° in the mouse lemur and the brown lemur. Leg adduction is due to thigh rotation about its longitudinal axis.

Kinematics of hind limb joints

The extent of overall limb flexion can be expressed as the percentage of functional limb length from the anatomical limb length. The hind limbs of the mouse lemur are most flexed relative to the other species. The functional hind limb length at touchdown is 66% and at lift-off 71% of the anatomical hind limb length. The most extended limbs were observed in the squirrel monkey. Both at touchdown and lift-off, functional hind limb lengths were 80% of the anatomical hind limb length. Hind limbs are normally more flexed at touchdown than at lift-off in the other three primate species.

In addition to the overall flexion of the hind limb, the limb undergoes a more or less deep flexion and a subsequent re-extension in the course of the support phase. This change of the functional limb length is called limb yield. This means that the hind limb bears weight and yields to hold the hip joint at an almost constant level. The extent of this yield can be expressed as the percentage of the shortest functional limb length at mid-support from the functional limb length at the beginning of a step cycle. Mid-support is defined as the moment when the point of ground contact passes underneath the hip joint. The yield of the hind limb is similar in the four species and independent of overall limb flexion and body weight. The percentage of functional hind limb length at mid-support from the functional limb length at touchdown is 84% in the mouse lemur and the squirrel monkey, 86% in the brown lemur and 90% in the cotton-top tamarin.

Protraction and retraction of the hind limb are mainly executed by femoral displacement in the hip joint. The hip joint is the only limb joint with a monophasic angular excursion during the step cycle, whereas knee and ankle joints display a biphasic angular excursion (Fig. 3). Thus, the hip joint is exclusively propulsive and does not assist in the compensation of vertical oscillations of the trunk. Hip joint extension starts immediately before touchdown and lasts until the end of the support phase. Thus, the difference between the touchdown angle and the lift-off angle of the hip joint corresponds to the joint amplitude, calculated as the difference between maximum and minimum joint angle (Table 4).

In the case of the knee and ankle joints, the difference between the touchdown angle and the lift-off angle (= effective joint movement; Fischer, 1994) is rather low compared with the joint amplitude, the difference between maximum and

Table 3. *Hind limb segments: angles at touchdown and lift-off, and the amplitude of excursion*

	Touchdown angle (deg.)		Lift-off angle (deg.)		Amplitude (deg.)	
	Mean ± S.D. (*N*)	Range	Mean ± S.D. (*N*)	Range	Mean ± S.D. (*N*)	Range
Thigh						
Microcebus murinus*	1±6 (76)	−12–27	76±9 (85)	53–96	78±9 (75)	40–98
Eulemur fulvus	1±6 (61)	−15–14	114±9 (61)	89–120	115±9 (31)	97–122
Saguinus Oedipus	11±8 (39)	−4–29	111±8 (37)	85–123	100±9 (33)	74–121
Saimiri sciureus*	31±5 (72)	24–39	90±8 (72)	78–107	61±9 (72)	55–78
Lower leg						
Microcebus murinus*	87±8 (76)	63–98	16±7 (76)	−5–33	71±9 (75)	56–98
Eulemur fulvus	85±9 (60)	64–106	17±9 (30)	2–31	72±9 (28)	64–82
Saguinus oedipus	78±7 (33)	61–91	4±5 (36)	−6–17	75±8 (31)	58–89
Saimiri sciureus*	103±2 (72)	98–107	23±3 (72)	17–27	80±7 (72)	64–99
Tarsometatarsus						
Microcebus murinus*	30±9 (77)	24–47	109±8 (77)	86–132	95±9 (67)	87–124
Eulemur fulvus	29±9 (37)	15–46	113±7 (30)	100–118	97±9 (28)	82–109
Saguinus oedipus	31±6 (24)	16–41	92±9 (24)	74–109	67±9 (24)	38–81
Saimiri sciureus*	37±5 (68)	24–47	93±6 (72)	80–108	60±9 (68)	42–87

*The asterisk denotes that these data are previously published (Fischer et al., 2002; Schmidt, 2005) and given here for comparison.

Table 4. *Hind limb joints: angles at touchdown and lift-off, and the amplitude of excursion*

	Touchdown angle (deg.)		Lift-off angle (deg.)		Amplitude (deg.)	
	Mean ± S.D. (N)	Range	Mean ± S.D. (N)	Range	Mean ± S.D. (N)	Range
Hip joint						
*Microcebus murinus**	43±6 (76)	27–54	113±9 (85)	85–135	75±7 (75)	56–92
Eulemur fulvus	56±6 (32)	45–69	145±8 (41)	131–161	92±6 (31)	83–106
Saguinus oedipus	51±5 (25)	44–61	155±9 (26)	116–168	106±8 (21)	93–120
*Saimiri sciureus**	70±5 (47)	61–78	130±5 (47)	120–140	76±9 (47)	65–91
Knee joint						
*Microcebus murinus**	88±7 (76)	68–109	92±9 (85)	60–129	30±8 (75)	15–54
Eulemur fulvus	86±9 (50)	49–116	120±9 (30)	98–129	60±9 (28)	38–74
Saguinus oedipus	89±7 (32)	75–101	114±9 (33)	82–130	38±7 (25)	23–47
*Saimiri sciureus**	132±4 (72)	122–141	110±7 (72)	98–121	35±7 (72)	24–54
Ankle joint						
*Microcebus murinus**	115±8 (77)	84–126	125±9 (77)	98–165	36±9 (67)	20–74
Eulemur fulvus	111±9 (20)	87–128	133±9 (20)	107–141	51±9 (20)	25–49
Saguinus oedipus	109±7 (25)	97–123	97±9 (25)	78–111	36±9 (22)	11–61
*Saimiri sciureus**	140±9 (68)	114–161	117±5 (72)	107–129	45±9 (68)	30–70

*The asterisk denotes that these data are previously published (Fischer et al., 2002; Schmidt, 2005) and given here for comparison.

minimum angle during the support phase. In all four primate species, the knee joint is strongly flexed during the first half of the support phase and is afterwards re-extended until the end of the support phase (Fig. 3). Maximum knee joint flexion coincides with the point of mid-support in the cotton-top tamarin and the squirrel monkey, when the ankle joint passes underneath the hip. It occurs early in the two prosimians, at the moment when the tip of the foot passes underneath the knee joint. The knee joint angle of the squirrel monkey is always greater than that of the other primates due to the more extended hind limbs at the beginning of the step cycle.

The angular excursion of the ankle joint during the support phase shows stronger variation between the species. The ankle joint of the cotton-top tamarin is much more flexed than that of the lemurs, but no flexion occurs in the ankle joint of the squirrel monkey. Angular excursion of the ankle joint is nearly identical in the two prosimian primates.

Pelvic movements and hip joint translation

The hip joint is the proximal pivot of the hind limb during walking. The pivot is not fixed in height. Extensive lateral bending and twisting movements of the lumbar spine change the pelvic position. Pelvic tilting about an anteroposterior axis alternately moves one hip joint below the other. Maximum downward tilt occurs towards the side that begins the support phase; the contralateral side, completing the support phase, is correspondingly tilted upwards. The second component of pelvic movement is a rotation about a vertical axis due to lateral bending of the lumbar spine. This rotation moves one hip joint ahead of the other. In summary, the hip joint of the hind limb at touchdown lies ahead of and below the hip joint of the contralateral hind limb that is beginning to take off. Sagittal bending of the lumbar spine, which moves the whole pelvis up and down, is less pronounced.

The prosimian primates studied here make extensive use of pelvic tilting and pelvic rotation to gain additional step length from horizontal hip translation (Table 5). These findings confirm previous observations by Shapiro et al. (2001) that lateral spine bending has an important functional role for gaining step length in walking primates. In the brown lemur, for example, a total horizontal translation of the hip joint of ~19 mm contributes 5% to the step length of the hind limb. The angle of the longitudinal pelvic axis to the horizontal plane as well as to the sacrum is more inclined in the primate species compared with other small mammals (Fischer et al., 2002). Mean touchdown angle of the pelvis relative to the horizontal

Table 5. *Pelvic angles at touchdown and lift-off, and horizontal hip joint translation*

	Touchdown angle (deg.)		Lift-off angle (deg.)		Hip joint translation (mm)	
	Mean ± S.D. (N)	Range	Mean ± S.D. (N)	Range	Mean ± S.D. (N)	% of step length
*Microcebus murinus**	42±6 (77)	25–60	37±5 (86)	26–49	3±1 (25)	4,3
Eulemur fulvus	55±5 (34)	43–64	41±6 (44)	31–58	19±3 (27)	5,1
Saguinus oedipus	59±4 (25)	48–67	55±4 (26)	35–75	8±1 (25)	2,8
*Saimiri sciureus**	38±4 (38)	25–45	36±3 (41)	29–49	10±1 (30)	2,3

*The asterisk denotes that these data are previously published (Fischer et al., 2002; Schmidt, 2005) and given here for comparison.

plane ranges between 38° in the squirrel monkey and 59° in the tamarin (Table 5). For comparison, the respective value in tree-shrews is 19° (Schilling and Fischer, 1999). Further personal observations have shown that in mammals that utilize synchronous gaits with extensive sagittal spine movements, the angle between the pelvis and the sacrum is rather flat. Thus, the pelvis is aligned with the line of action of the lumbar spine. The inclined pelvis in primates has a positive influence on gain step length in symmetrical rather than in synchronous gaits.

Hind limb proportions in quadrupedal primates and non-primate mammals

Scaling of hind limb length to body size

Fig. 4 shows the log-transformed scaling pattern of the hind limb length to body size in a sample of quadrupedal primates in comparison with other groups of mammals. Intensified sampling effort was made for small-sized taxa to permit comparisons of similarly sized animals across mammalian orders. Regression equations, confidence intervals for the allometry coefficients and correlation coefficients are noted under the graph (Fig. 4). Hind limb length is calculated as the sum of the lengths of the three functional hind limb segments: femur, tibia and tarsometatarsus.

The scaling of hind limb length to body size strongly varies
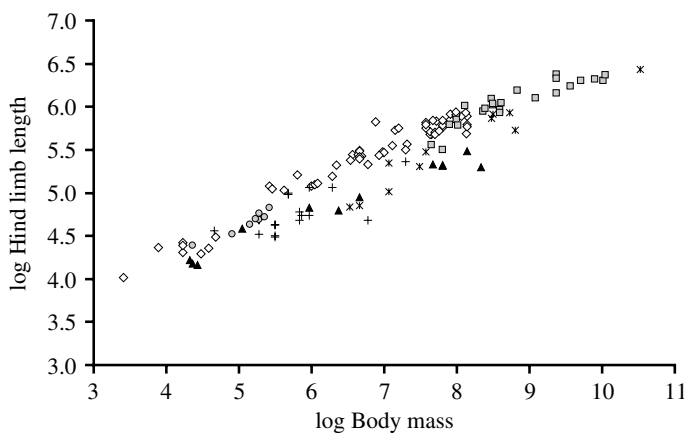
Group	N	a	b ± 95% C.I.	r
Primates, whole sample	83	2.881	0.366±0.018	**0.973**
◇ Strepsirhini + Platyrrhini	59	2.670	0.401±0.023	**0.976**
▫ Cercopithecinae	24	3.141	0.329±0.063	**0.899**
◎ Scandentia	7	2.670	0.380±0.168	**0.977**
+ Marsupialia	12	2.822	0.316±0.040	**0.984**
▲ Rodentia	14	2.558	0.380±0.193	0.674
Sciuridae	10	2.514	0.402±0.161	**0.879**
✻ Carnivora	10	1.994	0.438±0.088	**0.970**

Fig. 4. Log–log relationship between body mass and hind limb length in quadrupedal primates and other mammalian groups. Group-specific allometric relationships are estimated using the slope of the regression line (*b*), the surrounding 95% confidence intervals (C.I.) and the intersection with the *y*-axis (*a*). The correlation coefficient *r* is also given (bold style denotes significance, *P*<0.05).

among groups. Although slope values for the hind limb length in most taxa are greater than the isometric expectation of 0.33, they are significantly greater only in carnivores and in strepsirhine and platyrrhine primates, subsumed here into arboreal quadrupedal primates. Hind limb length of the primarily terrestrial quadrupedal cercopithecine monkeys scales close to isometry. The slope of the whole primate sample indicates a positive allometry for the hind limb, but the differences in hind limb scaling between arboreal and terrestrial primates are hidden by this estimation. The rodent sample also comprises species with different locomotor habitats (no significant correlation). Computation of the slope of the tree-dwelling sciurids provides a greater allometry coefficient and a statistically significant correlation coefficient. Tree-shrews also have relatively long hind limbs. The hind limb of marsupials scales close to isometry, also if the terrestrial taxa are removed from computation. Most of the slopes are not significantly different from each other. Significant differences exist only between the arboreal primates and the marsupials.

Obviously, small mammals exhibit consistent relationships between hind limb length and body size that do not appear to be influenced by locomotor mode or phylogeny. Hence, small primates, tree-shrews, small rodents and small marsupials all have similar size-related hind limb lengths, a pattern highly suggestive of functional constraint. Yet it is likely to represent a similar functional constraint experienced by the early members of their respective orders, as all are postulated to derive from small-bodied ancestral forms (Jenkins and Parrington, 1976; Luckett and Jacobs, 1980; Carroll, 1988; Gingerich et al., 1991; Dawson, 2003; Gebo, 2004).

Intralimb proportions of the hind limb

The limbs of quadrupedal mammals consist of three functional segments – the thigh, the lower leg and the foot. But, anthropomorphic indices, traditionally used to assess intralimb proportions in mammals, take only two limb segments into consideration. In the case of the hind limb, the crural index is normally used to calculate the proportional relationship between the thigh and the leg. In the following description, intralimb proportions are expressed as a percentage value of each segment length over the sum of the lengths of the three segments.

Fig. 5 shows that intralimb proportions of the hind limbs in quadrupedal mammals are fairly uniform. Intralimb proportions vary more among members of the same phylogenetic group than between different phylogenetic groups. Marsupials are distinct in that they possess relatively shorter feet in combination with longer lower legs. Observed divergence from the common pattern within a phylogenetic group is not generally related to size or to locomotor behaviour. The allometric relationship of the hind limb with respect to body size has no distinct effects on the proportional relationship of hind limb segments. The size-related increase of hind limb length in arboreal strepsirhines and platyrrhines does influence all three segments in the same fashion, or nearly
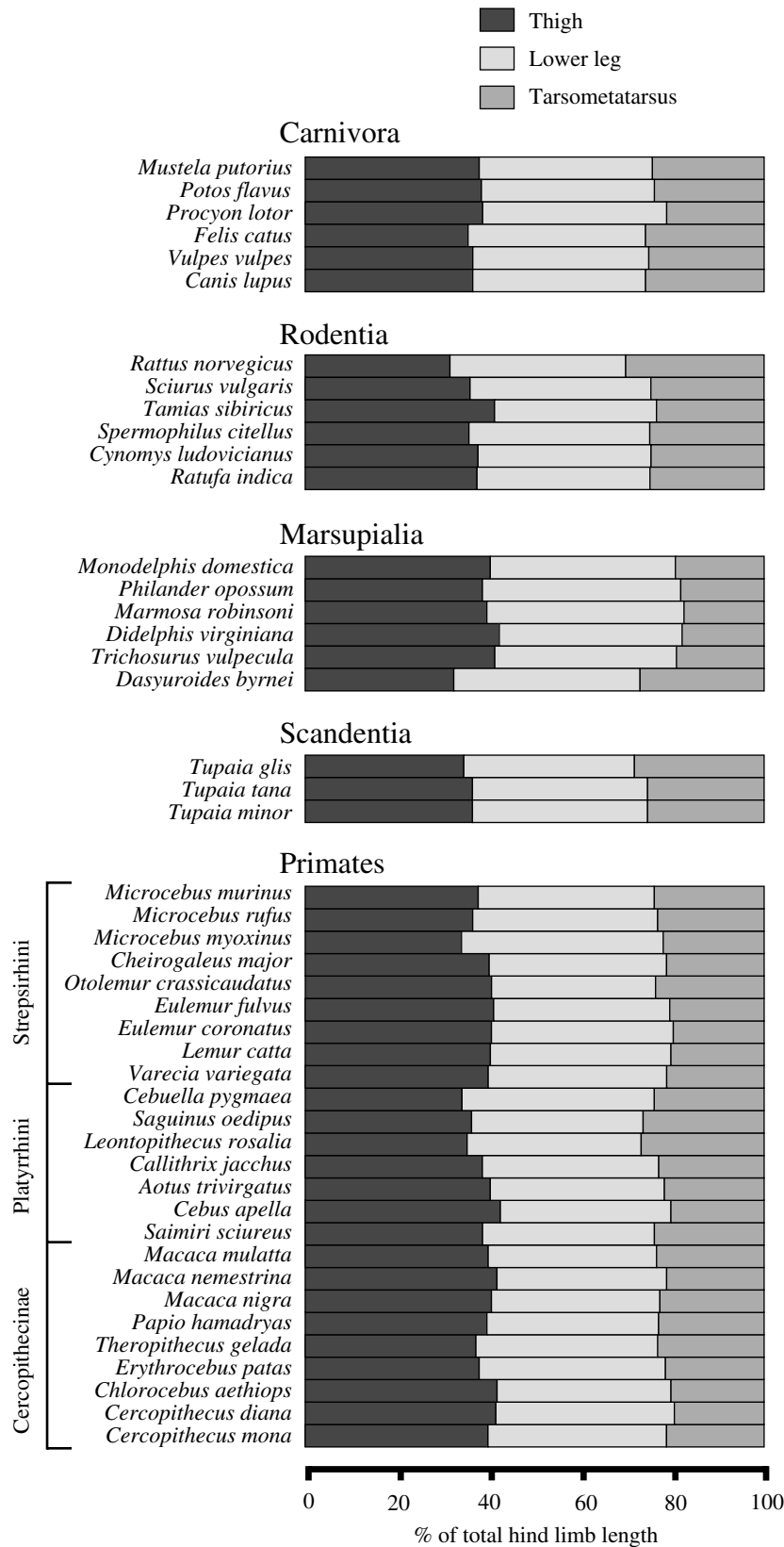
Fig. 5. Hind limb intralimb proportions in quadrupedal primates and other mammals. Proportional relationships between the three segments are expressed as the relative percentages of each segment length to the sum of the lengths of the segments (= total hind limb length).

so. No significant difference in intralimb proportions between the arboreal strepsirhines and platyrrhines and the terrestrial cercopithecines could be found. In the majority of primates, the percentage of the thigh length over the hind limb length ranges between 38% and 42%, and the percentage of the lower leg varies between 37% and 39%. The thigh is normally longer than the leg. Only the smallest primate included in the sample, the pygmy mouse lemur (31 g), has exceptionally long legs (44%) and short thighs (34%). Still, the best evidence that intralimb proportions of quadrupedal primates are size independent is that the hind limb of a mouse lemur, *Microcebus rufus* (70 g), is similar in proportions to the hind limb of the large gelada, *Theropithecus gelada* (20.5 kg). In tree-shrews, the relative length of the lower leg is the same as in primates, although the thigh is somewhat shorter (37%), and the foot is relatively longer (26%).

Discussion

Hind limb kinematics were compared during walking in four small arboreal quadrupedal primates. A large taxonomic sample was selected to help discriminate between size-related and phylogenetic aspects of hind limb movement. The primate sample included small-bodied taxa of both strepsirhine (mouse lemur) and platyrrhine (tamarin) clades that preserve purportedly 'primitive' postcranial characteristics, in addition to more derived representatives of each of these radiations (brown lemur and squirrel monkey, respectively). Recently, several authors have drawn attention to small body size, more 'primitive' morphologies and locomotor behaviour in their investigations of gait parameters in primate and non-primate mammals (Schmitt and Lemelin, 2002; Lemelin et al., 2003; Schmitt, 2003; Franz et al., 2005). This approach has substantially promoted our insight into the evolution of gait mechanics in primates, especially through the growing evidence of convergent evolutionary pathways in small arboreal marsupials.

Primates, like other mammals, change step length and frequency to change their walking speed. Consequently, limb kinematics are also speed dependent. The preferred walking speed of each animal was used to define equivalent mechanical and physiological situations so that comparison between different sized animals running at different speed was possible

(Hildebrand, 1966, 1985; Hoyt and Taylor, 1981; Perry et al., 1988; Larson et al., 2001).

Hind limb kinematics in primates and other mammals

Fig. 6 combines hind limb touchdown and lift-off postures of the four primates analyzed in this study with data from other primates, including the slender loris, two larger Old World monkeys, and a sample of other mammals (references given in the figure legend).

The touchdown position of the hind limb in the mouse lemur and the brown lemur is size independent and characterised by a horizontal thigh position and a vertical position of the lower leg. Demes et al. (1990) and Schmitt and Lemelin (2004) report the same touchdown position for the hind limb of the slow-climbing slender loris. The hind limb of the cotton-top tamarin is somewhat more retracted but the knee joint angle approaches 90°, as in prosimians. Larson et al. (2001) did not observe such a horizontal thigh position in their sample of arboreal quadrupedal primates. This may be an effect of different techniques used in movement analysis. The touchdown position of the hind limb in the mouse lemur, the brown lemur, the cotton-top tamarin and the slender loris resembles that of small non-cursorial mammals (Fig. 6). A horizontal placement of the thigh and a vertical leg position were observed in many mammals up to a body mass of 3.0 kg and, therefore, has been proposed to be a basic characteristic of mammalian locomotion (Jenkins, 1971; Fischer, 1994; Fischer et al., 2002). Due to the horizontal thigh position, the whole length of this long bone is immediately transmitted into step length. Correspondingly, due to the vertical position of the leg, the whole length of these long bones (tibia and fibula) is transmitted into the height of proximal pivot of the limb. Consequently, the lengthening of the hind limb with increasing body size by proportional lengthening of hind limb segments affects neither the touchdown position nor the protraction angle of the hind limb.

This principle is equivalent at lift-off, when the thigh is positioned vertically and the leg is horizontal. In this case, the increased length of the long bones would contribute the same degree to step length as to pivot height, and the total angular excursion of the limb would remain the same. Still, the lift-off position of the hind limb is obviously more variable than the touchdown position, perhaps relating to differences in thigh and leg length among taxa.

Only a few exceptions from this generalised pattern occur among smaller taxa (below 3.0 kg): in the tree-shrew, the hind limb is more strongly flexed at touchdown due to knee and
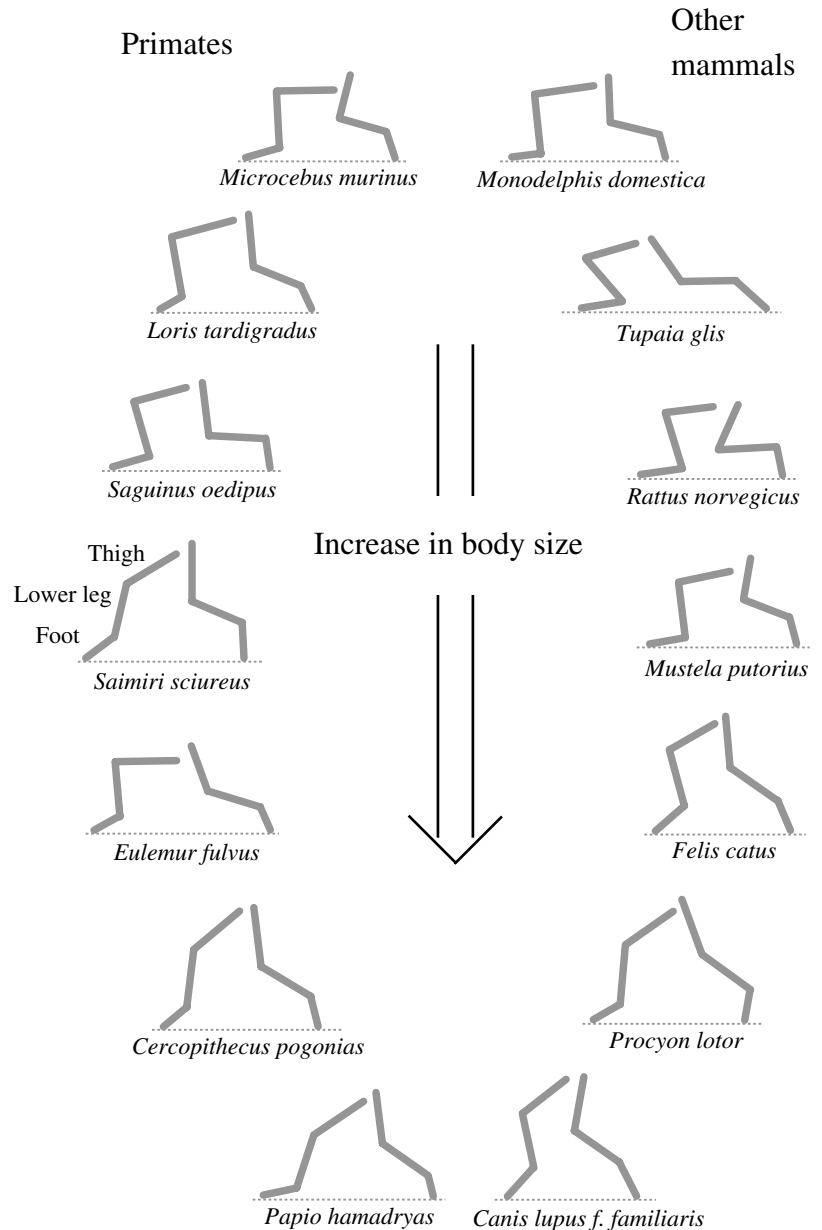

Fig. 6. Comparison of hind limb postures at touchdown and lift-off among quadrupedal primates and other mammals. Body masses range from 100 g (mouse lemur and shrew-like opossum) to 20 kg (dog) and 23 kg (baboon). Stick figure drawing data were compiled from Muybridge (1957), Jenkins (1971), Jenkins and Camazine (1977), Goslow et al. (1980), Meldrum (1991), Kuhtz-Buschbeck et al. (1994), Schilling and Fischer (1999), Fischer et al. (2002) and Schmitt and Lemelin (2004).

ankle joint angles below 90° (Schilling and Fischer, 1999). Hind limb protraction angle is thus very low (less than 30°), compensated for by the enormous retraction of the thigh and foot at the end of the support phase. In the laboratory rat, the thigh is less retracted, resulting in a more flexed lift-off position of the limb relative to the other mammals. Jenkins (1971) observed a similar crouched lift-off position in the Virginian opossum. Among primates, the squirrel monkey exhibits a more extended hind limb posture at touchdown than

do other similarly sized primates and non-primates. It is quite similar to larger cercopithecine primates. Another similarity to the cercopithecine monkeys is the nearly parasagittal displacement of the hind limbs in squirrel monkeys, whereas most other arboreal primates as well as non-cursorial non-primates abduct their thighs in the first half of the support phase. The peculiar hind limb kinematics of squirrel monkeys among small arboreal quadrupedal primates cannot be explained by the peculiarities of their skeletal locomotor apparatus regarding intra- and interlimb proportions, or allometric scaling of limb length or limb bone length. Even the load that the hind limb must bear is not much more than that of other arboreal primates (Schmidt, 2005). For the moment, the question of why hind limb kinematics in squirrel monkeys differ from those of other arboreal primates remains open.

Fig. 6 includes the hind limb posture of two Old World cercopithecine monkeys in comparison with larger carnivore species (Muybridge, 1957; Jenkins and Camazine, 1977; Goslow et al., 1981; Meldrum, 1991; Kuhtz-Buschbeck et al., 1994). The hind limbs of these larger mammals are generally more extended than in the smaller species, mainly due to a more inclined thigh position at touchdown (35–40° to the horizontal) and a more inclined position of the leg at lift-off. Additionally, the hind limbs of these five species move almost exclusively in a parasagittal plane. The guenon and the baboon protract their lower legs like the racoon but to a greater degree than the cat and the dog at the beginning of a step cycle, and therefore their hind limbs have a greater protraction angle. The vertical position of the thigh at the end of the support phase is a kinematic feature of arboreal primates that appears to be retained in terrestrial Old World monkeys. Jenkins and Camazine (1977) reported a similar thigh excursion for the cat and the red fox. Racoons exhibit greater retraction of the thigh. Such extended limb postures are usually said to be a biomechanical consequence of cursorial specialisation (Hildebrand, 1985; Stein and Casinos, 1997).

Primates and cursoriality

Cursoriality is a specific morpho-functional complex of features related to the specialization of the locomotor apparatus of animals for high-speed and long-lasting locomotion on the ground. Parasagittal limb excursions and more extended limb joints align the limb axis of cursorial mammals with the vector of the gravitational force and reduce the moment arms of the ground force vector acting on the limb joints (Biewener, 1983). Thus, bending stress acting upon the limb bones decreases with the adoption of an extended limb posture. Morphological traits usually associated with cursoriality include relatively long limbs, lengthened metapodials, shortened humeri/femora and a reduction in the number of distal limb bone elements (Steudel and Beattie, 1993; Lilje et al., 2003). Such cursorial adaptations evolved convergently with increasing body size in several lineages of mammals (rodents, carnivores, artiodactyls, perissodactyls). Terrestrial quadrupedal cercopithecine primates show cursorial-like limb kinematics, combined with other morphological adaptations. Hind limb length scales isometric to body size in order to have an equivalent limb length to the forelimbs. If limbs are extended, functional limb length approaches the anatomical limb length. In this case, limb flexion cannot be used to adopt an equivalent functional length of the fore and hind limb if limbs differ in their anatomical length. Unlike 'true' cursorial mammals, intralimb proportions of the hind limb do not change with changing limb kinematics in quadrupedal primates. Thus, length and excursion of the distal limb elements are not as important as they are in cursorial mammals for gaining pendular length and step length. Secondarily arboreal cercopithecine monkeys maintain most of these terrestrial adaptations. While travelling on arboreal substrates, the limbs of these monkeys are more flexed relative to ground walking (Schmitt, 1999) but they never attain the crouched posture exhibited by dedicated primate arborealists (Meldrum, 1991).

Angular excursion of the hind limb in primates and other mammals

Different kinematics of hind limb segments in quadrupedal primates and other mammals do not inevitably affect the total angular excursion of the hind limb. Table 6 shows hind limb excursion angles in quadrupedal primates in comparison with a sample of quadrupedal non-primate mammals. Total angular excursion is size independent in quadrupedal primates, varying between 73° (squirrel monkey) and 81° (slender loris). Larson et al. (2001) also report for their much broader sample of primates that hind limb excursion angles are fairly uniform within the order. Angular excursion of the hind limbs in the small-sized sample of other mammals is also independent of body size and may vary more in relation to data collection methodologies, as noted in Table 6. Comparisons among primates and other quadrupedal mammals in the size range between 50 g (spiny mouse) and 3.0 kg (Virginian opossum, brown lemur) show no definitive differences or similarities. The hind limb angular excursion of arboreal quadrupedal primates resembles that of tree-shrews and other non-cursorial primates and is far from being uniquely large, as proposed by Reynolds (1987) and Larson et al. (2001).

Interestingly, the contrasting interpretations of Reynolds (1987) and Larson et al. (2001) and those presented here are based upon similar observations, but the conclusion is different due to different comparative methods and different strategies in sample selection. Both Reynolds (1987) and Larson et al. (2001) paid more attention to the differences between typical primates and typical non-primate mammals. They are right that typical primates have larger hind limb angular excursions relative to typical non-primate species. But, these differences occur through the decrease of hind limb angular excursion as a part of convergent cursorial adaptations in the larger species of their sample of non-primate mammals, whereas larger quadrupedal primates maintain the hind limb angular excursion of their smaller ancestors. Hence primates as a clade do not exhibit uniquely large hind limb angular excursions; indeed, small primates exhibit angular excursions quite similar to those observed in other small mammals. Hind limb angular

Table 6. *Hind limb angular excursion in quadrupedal primates and other mammals*

Species	Total angular excursion (deg.)	Protraction angle (deg.)	Retraction angle (deg.)	Reference/notes
Primates				
Microcebus murinus	76±6	39±5	37±4	Rope-mill
Eulemur fulvus	74±5	33±3	41±3	Rope-mill
Eulemur fulvus	75			Reynolds (1987)
Loris tardigradus	81±7	35	40	Demes et al. (1990)
Nycticebus coucang	77±5			Demes et al. (1990)
Saguinus oedipus	77±4	36±4	42±3	Pole
Saimiri sciureus	73±5	37±4	36±3	Pole
Cercopithecus pogonias	62	34	28	After Meldrum (1991)
Cercopithecus neglectus	69	37	32	After Meldrum (1991)
Chlorocebus aethiops	72–85			Vilensky et al. (1988)
Papio hamadryas	71	38	33	After Muybridge (1957)
Papio hamadryas	75			Larson et al. (2001)
Non-primate mammals				
Monodelphis domestica	83±6	43±4	40±3	Pers. obs./treadmill
Didelphis virginiana	73	48	25	Jenkins (1971)
Acomys cahirinus	73±5	39±3	34±5	Pers. obs./pole
Acomys cahirinus	83±6	43±4	40±3	Pers. obs./treadmill
Rattus norvegicus	72±6	35±5	37±7	Pers. obs./runway
Rattus norvegicus	80±4	38±2	42±3	Pers. obs./treadmill
Galea musteloides	64±5	29±5	35±5	Pers. obs./runway
Galea musteloides	87±3	36±3	51±4	Pers. obs./treadmill
Tupaia glis	75±4	28±4	48±3	Pers. obs./pole
Tupaia glis	83±6	43±4	40±3	Pers. obs./treadmill
Felis catus	57	29	28	Kuhtz-Buschbeck et al. (1994)
Procyon lotor	71	33	38	Jenkins and Camazine (1977)
Canis lupus f. familiaris	44	28	16	Goslow et al. (1981)

excursion would be uniquely large in primates only if ancestral primates exhibited significantly larger angular excursions than did their non-primate sister taxa. In an evolutionary sense, it would seem that the derived limb excursions actually belong to the non-primate cursors that have exchanged larger angular excursions for enhanced stability of longer limbs.

Conclusions

The specific characteristics of primate locomotion evolved in small arboreal quadrupedal mammals with a body mass of less than 100 g. Therefore, some living small arboreal primates can serve as reliable models to study the basic characteristics of primate locomotion. The comparison of such species with tree-shrews and other non-cursorial small mammals thought to possess the ancestral pattern of mammalian locomotion enables the differentiation between derived, primate-specific locomotor characteristics and functional or ancestral traits common to small mammals in general.

Hind limb kinematics of arboreal quadrupedal prosimians are size independent and resemble those of small non-cursorial mammals. Plesiomorphic characteristics include the horizontal position of the thigh and the vertical position of the lower leg at touchdown. At lift-off, the thigh is vertically oriented and the leg is nearly horizontal. This initial pattern is independent of the actual anatomical length of the hind limb. In arboreal primates, hind limb length scales with strong positive allometry to body size, but intralimb proportions do not change with increasing size. Step length and pivot height increase to the same degree by the proportional lengthening of limb bones. Thus, total angular excursion of the hind limb in arboreal primates remains equal to other non-cursorial mammals and is far from being uniquely large in primates, as previously proposed by Reynolds (1987) and Larson et al. (2001). Terrestrial primates alter hind limb kinematics through the adoption of more extended joint postures, whereas intralimb proportions and total angular excursions remain equal to small arboreal ancestors. The observed difference in angular excursion between large primate and non-primate mammals probably stems from the decreasing excursion angle of the limbs as part of cursorial adaptations in several phylogenetic lineages of mammals.

References

Aiello, L. C. (1981). The allometry of primate body proportions. *Symp. Zool. Soc. Lond.* **48**, 331-358.

Alexander, R. McN. and Maloiy, G. M. O. (1984). Stride length and stride frequencies of primates. *J. Zool. Lond.* **29**, 577-582.

Alexander, R. McN., Jayes, A. S., Maloiy, G. M. O. and Wathuta, E. M. (1979). Allometry of the limb bones of mammals from shrews (*Sorex*) to elephant (*Loxodonta*). *J. Zool. Lond.* **189**, 305-314.

Arms, A., Voges, V., Fischer, M. S. and Preuschoft, H. (2002). Arboreal locomotion in small New-World monkeys. *Z. Morph. Anthropol.* **83**, 243-263.

Beard, K. C. (1993). Phylogenetic systematics of the Primatomorpha, with special reference to Dermoptera. In *Mammal Phylogeny: Placentals* (ed. F. S. Szalay, M. J. Novacek and M. C. McKenna), pp. 129-150. New York: Springer Verlag.

Bertram, J. E. A. and Biewener, A. A. (1990). Differential scaling of the long bones in the terrestrial Carnivora and other mammals. *J. Morph.* **204**, 157-169.

Biewener, A. A. (1983). Locomotory stresses in the limb bones of two small mammals: the ground squirrel and chipmunk. *J. Exp. Biol.* **103**, 131-154.

Carroll, R. L. (1988). *Vertebrate Paleontology and Evolution.* New York: W. H. Freeman and Company.

Cartmill, M. (1972). Arboreal adaptations and the origin of the order Primates. In *Functional and Evolutionary Biology of Primates* (ed. R. Tuttle), pp. 97-122. Chicago: Aldine Atherton.

Cartmill, M. (1974). Pads and claws in arboreal locomotion. In *Primate Locomotion* (ed. F. A. Jenkins, Jr), pp. 45-83. New York: Academic Press.

Cartmill, M., Lemelin, P. and Schmitt, D. (2002). Support polygons and symmetrical gaits in mammals. *Zool. J. Linn. Soc.* **136**, 401-420.

Christiansen, P. (1999). Scaling of mammalian long bones: small and large mammals compared. *J. Zool. Lond.* **247**, 333-348.

Cronin, J. E. and Sarich, V. M. (1980). Tupaiid and Archonta phylogeny: the macromolecular evidence. In *Comparative Biology and Evolutionary Relationships of Tree Shrews* (ed. W. P. Luckett), pp. 293-312. New York: Plenum Press.

Dawson, M. R. (2003). Paleogene rodents of Eurasia. *Deinsea* **10**, 97-126.

Demes, B., Jungers, W. L. and Nieschalk, U. (1990). Size- and speed-related aspects of quadrupedal walking in slender and slow lorises. In *Gravity, Posture and Locomotion in Primates* (ed. F. K. Jouffroy, M. H. Stack and C. Niemitz), pp. 175-197. Florence: Il Sedicesimo.

Demes, B., Larson, S. G., Stern, J. T., Jr, Jungers, W. L., Biknevicius, A. R. and Schmitt, D. (1994). The kinetics of primate quadrupedalism: "hindlimb drive" reconsidered. *J. Hum. Evol.* **26**, 353-374.

Fischer, M. S. (1994). Crouched posture and high fulcrum. A principle in the locomotion of small mammals: the example of the rock hyrax (*Procavia capensis*) (Mammalia: Hyracoidea). *J. Hum. Evol.* **26**, 501-524.

Fischer, M. S., Schilling, N., Schmidt, M., Haarhaus, D. and Witte, H. (2002). Basic limb kinematics of small therian mammals. *J. Exp. Biol.* **205**, 1315-1338.

Fleagle, J. G. (1999). *Primate Adaptation and Evolution.* San Diego, CA: Academic Press.

Fleagle, J. G. and Mittermeier, R. (1980). Locomotor behavior, body size, and comparative ecology of seven Surinam monkeys. *Am. J. Phys. Anthropol.* **52**, 301-314.

Franz, T. M., Demes, B. and Carlson, K. J. (2005). Gait mechanics of lemurid primates on terrestrial and arboreal substrates. *J. Hum. Evol.* **48**, 199-217.

Garber, P. A. (1980). Locomotor behavior and feeding ecology of the Panamanian tamarin (*Saguinus oedipus geoffroyi*, Callitrichidae, Primates). *Int. J. Primatol.* **1**, 185-201.

Garbutt, N. (1999). *Mammals of Madagascar.* New Haven, London: Yale University Press.

Gebo, D. J. (1987). Locomotor diversity in Prosimian Primates. *Am. J. Primat.* **13**, 271-281.

Gebo, D. L. (2004). A shrew-sized origin for primates. *Yrbk. Phys. Anthropol.* **47**, 40-62.

Gingerich, P. D., Dashzeveg, D. and Russell, D. E. (1991). Dentition and systematic relationships of *Altanius orlovi* (Mammalia, Primates) from the early Eocene of Mongolia. *Geobios* **24**, 637-646.

Goslow, G. E., Jr, Seeherman, H. J., Taylor, C. R., McCutchin, M. N. and Heglund, N. C. (1981). Electrical activity and relative length changes of dog limb muscles as a function of speed and gait. *J. Exp. Biol.* **94**, 15-42.

Grzimek, B. (1987). *Enzyklopädie der Säugetiere* (ed. R. Kleienburg). München: Kindler Verlag.

Hershkovitz, P. (1977). *Living New World Monkeys (Platyrrhini) With an Introduction To Primates*, vol. 1. Chicago: University of Chicago Press.

Hildebrand, M. (1966). Analysis of the symmetrical gaits of tetrapods. *Folia Biotheor.* **6**, 9-22.

Hildebrand, M. (1967). Symmetrical gaits of primates. *Amer. J. Phys. Anthropol.* **26**, 119-130.

Hildebrand, M. (1985). Walking and running. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. M. Bramble, K. F. Liem and D. B. Wake), pp. 38-57. Cambridge, MA, London: The Belknap Press of Harvard University Press.

Hoyt, D. F. and Taylor, C. R. (1981). Gait and energetics of locomotion in horses. *Nature* **292**, 239-240.

Ishida, H., Jouffroy, F. K. and Nakano, Y. (1990). Comparative dynamics of pronograde and upside down horizontal quadrupedalism in the slow loris (*Nycticebus coucang*). In *Gravity, Posture and Locomotion in Primates* (ed. F. K. Jouffroy, M. H. Stack and C. Niemitz), pp. 209-220. Florence: Il Sedicesimo.

Jenkins, F. A., Jr (1971). Limb posture and locomotion in the Virginia opossum (*Didelphis marsupialis*) and in other non-cursorial mammals. *J. Zool. Lond.* **165**, 303-315.

Jenkins, F. A., Jr (1974). Tree shrew locomotion and the origins of primate arborealism. In *Primate Locomotion* (ed. F. A. Jenkins, Jr), pp. 85-115. New York: Academic Press.

Jenkins, F. A., Jr and Camazine, S. M. (1977). Hip structure and locomotion in ambulatory and cursorial carnivores. *J. Zool. Lond.* **181**, 351-370.

Jenkins, F. A., Jr and Parrington, F. R. (1976). The postcranial skeletons of the triassic mammals *Eozostrodon*, *Megazostrodon* and *Erythrotherium*. *Phil. Trans. Roy. Soc. Lond.* **273**, 387-431.

Jungers, W. L. (1985). Body size and scaling of limb proportions in primates. In *Size and Scaling in Primate Biology* (ed. W. L. Jungers), pp. 345-381. New York: Plenum Press.

Jungers, W. L. and Fleagle, J. G. (1980). Postnatal growth allometry of the extremities in *Cebus albifrons* and *Cebus apella*: a longitudinal and comparative study. *Am. J. Phys. Anthropol.* **53**, 471-478.

Kimura, T., Okada, M. and Ishida, H. (1979). Kinesiological characteristics of primate walking: its significance in human walking. In *Environment, Behavior, and Morphology: Dynamic Interactions in Primates* (ed. M. E. Morbeck, H. Preuschoft and N. Gomberg), pp. 297-311. New York: Gustav Fischer.

Kuhtz-Buschbeck, J. P., Boczek-Funke, A., Illert, M. and Weinhardt, G. (1994). X-ray study of the cat hindlimb during treadmill locomotion. *Eur. J. Neurosci.* **6**, 1187-1198.

Lammers, A. R. and German, R. Z. (2002). Ontogenetic allometry in the locomotor skeleton of specialized half-bounding mammals. *J. Zool. Lond.* **258**, 485-495.

Larney, E. and Larson, S. G. (2004). Compliant walking in primates: elbow and knee yield in primates compared to other mammals. *Am. J. Phys. Anthropol.* **125**, 42-50.

Larson, S. G., Schmitt, D., Lemelin, P. and Hamrick, M. (2000). Uniqueness of primate forelimb posture during quadrupedal locomotion. *Am. J. Phys. Anthropol.* **112**, 87-101.

Larson, S. G., Schmitt, D., Lemelin, P. and Hamrick, M. (2001). Limb excursion during quadrupedal walking: how do primates compare to other mammals? *J. Zool. Lond.* **255**, 353-365.

Lemelin, P., Schmitt, D. and Cartmill, M. (2003). Footfall patterns and interlimb co-ordination in opossums (Family Didelphidae): evidence for the

evolution of diagonal-sequence walking gaits in primates. *J. Zool. Lond.* **260**, 423-429.

Lilje, K. E., Tardieu, C. and Fischer, M. S. (2003). Scaling of long bones in ruminants with respect to the scapula. *J. Zool. Syst. Evol. Res.* **41**, 118-126.

Luckett, W. P. and Jacobs, L. L. (1980). Proposed fossil tree shrew genus *Palaeotupaia*. *Nature* **288**, 104.

Martin, R. D. (1973). A review of the behaviour and ecology of the lesser mouse lemur (*Microcebus murinus* J. F. Miller, 1777). In *Comparative Ecology and Behaviour of Primates* (ed. R. P. Michael and J. H. Crook), pp. 1-68. London: Academic Press.

McCrossin, M. L., Benefit, B. R., Gitau, S. N., Palmer, A. K. and Blue, K. T. (1998). Fossil evidence for the origin of terrestriality among Old World higher primates. In *Primate Locomotion. Recent Advances* (ed. E. Strasser, J. G. Fleagle, A. Rosenberger and H. McHenry), pp. 353-395. New York: Plenum Press.

Meldrum, D. J. (1991). Kinematics of the cercopithecine foot on arboreal and terrestrial substrates with implications for the interpretation of hominid terrestrial adaptations. *Am. J. Phys. Anthropol.* **84**, 273-289.

Muybridge, E. (1957). *Animals in Motion* (ed. L. S. Brown), pp. 1-75. New York: Dover. (Originally published by Chapman and Hall, London, 1899.)

Nowak, R. M. (1999). *Walker's Mammals of the World.* Sixth edition. Baltimore, London: The Johns Hopkins University Press.

Perry, A. K., Blickhan, R., Biewener, A. A., Heglund, N. C. and Taylor, C. R. (1988). Preferred speeds in terrestrial vertebrates: are they equivalent? *J. Exp. Biol.* **137**, 207-219.

Rasmussen, D. T. (1990). Primate origins: lessons from a Neotropical marsupial. *Am. J. Primatol.* **22**, 263-277.

Reynolds, T. R. (1985). Mechanics of increased support of weight by the hindlimbs in primates. *Am. J. Phys. Anthropol.* **67**, 335-349.

Reynolds, T. R. (1987). Stride length and its determinants in humans, early hominids, primates, and mammals. In *Primate locomotion* (ed. F. A. Jenkins, Jr), pp. 171-200. New York: Academic Press.

Roth, V. L. (1984). How elephants grow: heterochrony and the calibration of developmental stages in some living and fossil species. *J. Vertebrate Palaeontol.* **4**, 126-145.

Rowe, N. (1996). *The Pictorial Guide to the Living Primates.* Charlestown, RI: Pogonias Press.

Schilling, N. and Fischer, M. S. (1999). Kinematic analysis of treadmill locomotion of tree shrews, *Tupaia glis* (Scandentia: Tupaiidae). *Z. Säugetierk.* **64**, 129-153.

Schmidt, M. (2005). Quadrupedal locomotion in squirrel monkeys (Cebidae: *Saimiri sciureus*) – a cineradiographic study of limb kinematics and related substrate reaction forces. *Am. J. Phys. Anthropol.* doi:10.1002/ajpa/20089

Schmidt, M. and Fischer, M. S. (2000). Cineradiographic study of forelimb movements during quadrupedal walking in the brown lemur (*Eulemur fulvus*, Primates: Lemuridae). *Am. J. Phys. Anthropol.* **111**, 245-262.

Schmitt, D. (1999). Compliant walking in primates. *J. Zool. Lond.* **248**, 149-160.

Schmitt, D. (2003). Evolutionary implications of the unusual walking mechanics of the common marmoset (*C. jacchus*). *Am. J. Phys. Anthropol.* **122**, 28-37.

Schmitt, D. and Larson, S. G. (1995). Heel contact as a function of substrate type and speed in primates. *Am. J. Phys. Anthropol.* **96**, 39-50.

Schmitt, D. and Lemelin, P. (2002). Origins of primate locomotion: gait mechanics of the woolly opossum. *Am. J. Phys. Anthropol.* **118**, 231-238.

Schmitt, D. and Lemelin, P. (2004). Locomotor mechanics of the slender loris (*Loris tardigradus*). *J. Hum. Evol.* **47**, 85-94.

Shapiro, L. J., Demes, B. and Cooper, J. (2001). Lateral bending of the lumbar spine during quadrupedalism in strepsirhines. *J. Hum. Evol.* **40**, 231-259.

Sokal, R. R. and Rohlf, F. J. (1995). *Biometry: The Principles and Practice of Statistics in Biological Research.* Third edition. San Francisco: W. H. Freeman and Company.

Stein, B. R. and Casinos, A. (1997). What is a cursorial mammal? *J. Zool. Lond.* **242**, 185-192.

Steudel, K. and Beattie, J. (1993). Scaling of cursoriality in mammals. *J. Morph.* **217**, 55-63.

Sussman, R. W. and Kinzey, W. G. (1984). The ecological role of the Callitrichidae: a review. *Am. J. Phys. Anthropol.* **64**, 419-449.

Tattersall, I. (1977). Ecology and behavior of *Lemur fulvus mayottensis*. *Anthropol. Papers Am. Mus. Nat. Hist.* **54**, 421-482.

Thorington, R. W., Jr (1968). Observations of squirrel monkeys in a Colombian forest. In *The Squirrel Monkey* (ed. L. A. Rosenblum and R. W. Cooper), pp. 69-85. New York: Academic Press.

Turnquist, J. E. and Wells, J. P. (1994). Ontogeny of locomotion in rhesus macaques (*Macaca mulatta*): I. Early postnatal ontogeny of the musculoskeletal system. *J. Hum. Evol.* **26**, 487-499.

Vilensky, J. A. and Larson, S. G. (1989). Primate locomotion: utilization and control of symmetrical gaits. *Annu. Rev. Anthropol.* **18**, 17-35.

Vilensky, J. A., Gankiewicz, E. and Townsend, D. W. (1988). Effect of size on vervet (*Cercopithecus aethiops*) gait parameters: A cross-sectional approach. *Am. J. Phys. Anthropol.* **76**, 463-480.

Walker, A. C. (1974). Locomotor adaptations in the past and present prosimian primates. In *Primate locomotion* (ed. F. A. Jenkins, Jr), pp. 349-382. New York: Academic Press.

Wible, J. R. and Covert, H. H. (1987). Primates: cladistic diagnosis and relationships. *J. Hum. Evol.* **16**, 1-22.

Zar, J. H. (1968). Calculation and miscalculation of the allometric equation as a model in biological data. *BioScience* **18**, 1118-1120.