

Ontogenetic development of locomotion in small mammals – a kinematic study

Nadja Schilling

Institut für Spezielle Zoologie und Evolutionsbiologie, Friedrich-Schiller-Universität, Erbertstr. 1, 07743 Jena, Germany

e-mail: nadja.schilling@uni-jena.de

Accepted 29 August 2005

Summary

Comparative studies of locomotion indicate that limb design and performance are very similar in adult mammals of small to medium size. The present study was undertaken to test whether basic therian limb pattern is present during postnatal development. Kinematic data were collected from juveniles of two eutherian species in a cross-sectional study, using cinevideography. The tree shrew *Tupaia glis* and the cui *Galea musteloides* were selected because of their different reproductive strategies, which could result in differences in the development of locomotor abilities. The aims of this study were to describe the process by which young animals develop the adult pattern of locomotion and the extent to which this process varies in two species with very different postnatal ontogenies.

Despite their different life histories, the development of kinematic parameters in the altricial tree shrew and the precocial cui are surprisingly similar. General limb design, performance, and timing of segment and joint movements in the young animals were similar to adults in both species, even from the first steps. Touch-down of the forelimb occurred at the position below the eye in all individuals and limb position was highly standardized at touch-down; no major changes in segment and joint angles were observed. Significant changes occurred at lift-

off. With increasing body mass, limb segments rotated more caudally, which resulted in larger limb excursions and relatively longer steps. Developmental changes in locomotor abilities were similar in both species; only the time necessary to reach the adult performance was different. Despite the widely assumed maturity of locomotor abilities in precocial young, the first steps of the cui juveniles were not similar to the movements of adults. The adult locomotor pattern was reached within the first postnatal week in the cui and by the time they leave the nest in the tree shrew (39 days after birth; individual P39).

These results suggest that during the evolution of precocial development only processes independent of exercise or gravity can be shifted into the intrauterine period. However, development of locomotor ability depends on exercise, and adjustments and training occur during growth. Therefore, only the time necessary to reach maturity was clearly shortened in the precocial juvenile relative to the ancestral altricial condition.

Key words: altricial, precocial, postnatal, limb movement, symmetrical gait, X-ray, tree shrew, *Tupaia glis*, cui, *Galea musteloides*.

Introduction

Limb design and limb movement patterns appear to be very similar in small to medium-sized mammals (Fischer et al., 2002). All species investigated show similar limb performance independent of their taxonomic position, including *Metatheria*: Dasyuridae, Didelphidae, and *Eutheria*: Rodentia, Lagomorpha, Hyracoidea, Artiodactyla, Scandentia, Primates (Fischer, 1994, 1999; Fischer and Lehmann, 1998; Schilling and Fischer, 1999; Schmidt and Fischer, 2000; Fischer et al., 2002). Kinematic and dynamic similarities at different gaits and velocities support the uniformity of limb posture and performance (Fischer et al., 2002; Witte et al., 2002).

The functional correspondence of limb elements has changed because of the transition from the two-segmented limb design in reptiles to three-segment limbs in mammals. In symmetrical gaits, the scapula corresponds functionally to the

femur, the humerus to the shank and the lower arm plus hand to the foot (Fischer, 1994; Fischer et al., 2002). These three limb segments are arranged in a zigzag configuration in the basic therian limb (Fischer and Witte, 1998). Vertical fluctuations of the body centre of mass and torsions along the body axis can be avoided by using these double flexed pendulums. Most of the limb displacement is caused by movements of the proximal segments. The distal segments contribute less to total step length. Pivots of the fore- and hindlimbs (scapular fulcrum and hip joint) are at nearly the same height, resulting in similar functional pendulum lengths. At touch-down, the femur is positioned parallel to ground and at lift-off the humerus and shank are nearly horizontal. Because of the evolutionary 'new' functional correspondence of limb segments of the mammalian fore- and hindlimbs, and despite

the serial homologies, the kinematics of the shoulder blade must be compared with the femur, the humerus with the shank, and the lower arm and hand with the foot and toes.

All previous studies were undertaken on adult animals. Therefore, the question arose as to whether these characteristics of basic limb design and performance change during ontogenetic development. Ontogenetic studies of kinematic parameters of mammals are rare. Developmental changes in limb position have been described only for *Rattus norvegicus* and *Felis catus* f. *domestica* (Peters, 1983; Westerga and Gramsbergen, 1990; Jamon and Clarac, 1998; Howland et al., 1995). Changes in hindlimb joint angles during development were investigated in *Cercopithecus aethiops* (Vilensky and Gankiewicz, 1989). These studies utilized normal video recordings in which limb movements, especially of proximal limb segments, are hidden under fur, skin, soft tissues and muscles. Cineradiography is the only tool that allows accurate analysis of limb segment and joint movements. This study is the first attempt to analyse limb movements during ontogenetic development using cineradiography.

Because altricial and precocial development could result in different patterns of limb use during postnatal growth, two species were chosen for analysis. The tree shrew *Tupaia glis* gives birth to typical altricial juveniles, whereas the cui *Galea musteloides* has precocial young that walk immediately after birth. Only the kinematic changes of symmetrical gaits were studied, because the walk and trot arise first during ontogeny in different mammalian species independent of their preferred gait as adults (*Felis catus* f. *domestica*: Peters, 1983; Bradley and Smith, 1988a,b; *Rattus norvegicus*: Altman and Sudarshan, 1975; Geisler et al., 1993; *Macaca fuscata*: Nakano, 1996; *Gerbillus dasyurus*: Blumberg-Feldman and Eilam, 1995; *Jaculus orientalis*: Eilam and Shefer, 1997; *Microtus socialis*, *Meriones tristrami*, *Eliomys melanurus*: Eilam, 1997). The aims of the present study were to investigate the development of locomotion in order to describe the process by which the adult pattern of locomotion emerges and to determine the time of onset of adult limb performance.

Materials and methods

Animals

This study was undertaken on cuis (Rodentia: Caviidae: *Galea musteloides* Meyen 1833) and tree shrews (Scandentia: Tupaiidae: *Tupaia glis* Diard 1820, *Tupaia belangeri* Wagner 1841). All cuis were obtained from our own laboratory. Tree shrew juveniles (*Tupaia belangeri*) were kindly provided by the German Primate Centre at Göttingen, Germany (Prof. Dr E. Fuchs). Adult animals (*Tupaia glis*) were from the breeding colony of Prof. Dr H.-R. Duncker at Gießen University. Because of the taxonomic confusion of the (sub)species *Tupaia belangeri* and *Tupaia glis* (Dene et al., 1978; Honacki et al., 1982), these species will be considered together in this study.

The species were selected because of their comparable body size, similar adult kinematics and different reproductive

biology. Although the two species differ in their habitats, cuis living underground in open grasslands while tree shrews are arboreal, both species have comparable limb design and performance (Schilling and Fischer, 1999; Fischer et al., 2002). As Jenkins (1974) pointed out, for small animals like tree shrews, tree branches are relatively thick and impose the same demands for locomotion as does the ground in terrestrial species. Locomotor differences resulting from the presence or absence of the tail in the tailed tree shrew and tail-less cui were not addressed in the current study, because differences in kinematics and dynamics between tailed and tail-less species are only relevant to asymmetrical gaits such as the gallop or half bound, in which extensive sagittal spine movements occur (Schilling et al., 1999; Fischer et al., 2002), or during arboreal or non-level locomotion.

Table 1. Postnatal age, body mass and sex of all investigated individuals

Age (days)	Body mass (g)	Sex	Litter size (m/f)
<i>Galea musteloides</i>			
0	44.0	f	2/1
1	38.0	m	2/1
2	34.0	m	2/1
5	50.8	m	2/1
6	43.7	m	2/2
7	41.9	f	2/2
8(1)	47.0	f	2/1
8(2)	65.6	f	2/2
9	53.5	m	2/2
21	113.0	m	1/2
22	97.3	f	1/2
33	165.8	f	1/2
34	157.1	m	2/1
Ad(1)	139.8	f	1/2
Ad(2)	206.6	m	1/2
<i>Tupaia glis</i>			
14	63.7	f	1/1
21	84.9	m	1/0
23	94.4	f	2/1
25	121.0	f	1/1
30	132.9	m	1/1
31	124.2	f	1/2
33	87.8	f	2/1
34	142.1	f	1/2
37	105.0	f	3/1
39(1)	146.3	f	2/1
39(2)	71.6	f	3/2
Ad(1)	151.0	f	–
Ad(2)	210.0	m	–

f, female; m, male; Ad, adult.

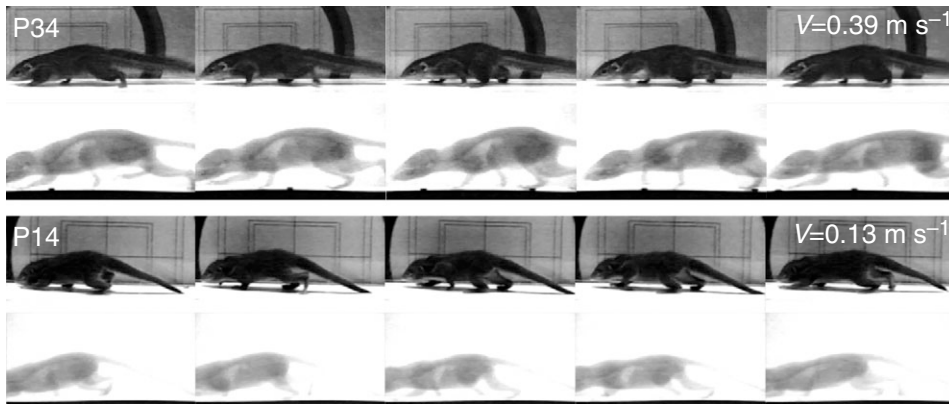
Litter size may have an impact on body mass so is included.

Day of birth corresponds to P0. The two adult individuals of both species are named Ad(1) and Ad(2), and the two 8 day (*G. musteloides*) and 39 day (*T. glis*) animals 8(1), 8(2) and 39(1), 39(2), respectively.

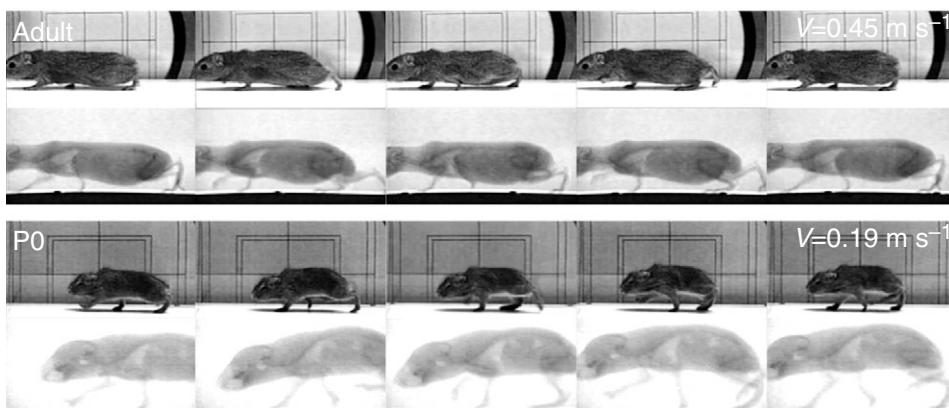
Limb kinematics of *cuis* were investigated in previous studies using a different experimental set up (Fischer, 1999; Fischer et al., 2002). New data were collected to guarantee the use of the same protocol for all subjects. Locomotor parameters of adult tree shrews from a previous study, which included more detailed information about metric parameters, footfall patterns, gait dependent kinematics, intervertebral sagittal spine movements and intralimb timing, were included to increase the sample size (Schilling and Fischer, 1999).

Juvenile data were recorded from the age when the first successive steps with a lifted belly occurred until no differences between locomotor parameters of juveniles and adults were found (adult locomotor pattern). Adulthood was defined by sexual maturity. Age, body mass, sex and litter size of all investigated individuals are given in Table 1. In a few age stages, two individuals were included to test whether locomotor parameters change with chronological age or with body mass during postnatal development. All locomotor data were recorded in one day and the animals were not previously trained to walk on the treadmill. After recording their locomotion, animals were killed and further processed anatomically and histologically (Schilling and Fischer, 2001; N. Schilling and A. Petrovitch, manuscript submitted for publication). All procedures were approved by the Committee for Animal Protection of the state of Thuringia, Germany.

A *Tupaia glis*



B *Galea musteloides*



Kinematic recording

Limb movements were studied by high-speed-cinevideography (150 frames s^{-1}) recorded at the IWF Knowledge and Media gGmbH at Göttingen, Germany (Fig. 1). The X-ray system consisted of an automatic X-ray source image amplifier chain (Phillips 9807 501 800 01, Germany). Pulsed X-ray shots (57–82 kV, 200 mA) were applied. Images from walking animals in lateral perspective were recorded from the image amplifier using one of three synchronous working cameras of the high-speed video-system Camsys® (Mikromak Service K. Brinkmann, Berlin, Germany; Fig. 1). The other two cameras recorded the animal's motion in cranial and lateral perspectives to verify that the locomotion occurred parallel to the image amplifier.

Animals walked on a horizontal motor-driven treadmill within a Perspex enclosure (100 cm \times 45 cm \times 11 cm). Treadmill speed was held relatively constant during X-ray shots (mean coefficient of variation of animal's speed: 0.19). No attempt was made to record either acceleration or deceleration; rather, animals moved at their preferred 'travel speed'. Recording time was limited by the memory capacity of Camsys® (6.83 s). The size of the image amplifier (20 cm \times 15 cm) only allowed for synchronous recording of all four limbs in the younger and smaller animals. Fore- and hindlimbs had to be filmed separately in older animals. An orthogonal wire grid placed perpendicular to the projection plane and at the position of the animals sagittal plane while on the treadmill provided reference points for motion analysis and correction of geometric distortions.

Motion analysis

The analogue videotapes were converted using a video processing board ('Screen machine I', FAST Multimedia AG, Munich, Germany). Of the video sequences, only trials with continuous motion and several successive steps were used. Since treadmill speed was held relatively constant during X-ray shots, animals velocity was also nearly constant during a given sequence. Skeletal landmarks were interactively captured and their x - and y -coordinates used to define

Fig. 1. Frames of video and high-speed cinevideography of mature and youngest individuals of (A) *Tupaia glis* and (B) *Galea musteloides*. P0 = day of birth; P34 and P14 = 34 and 14 days after birth, respectively. V , velocity ($m s^{-1}$).

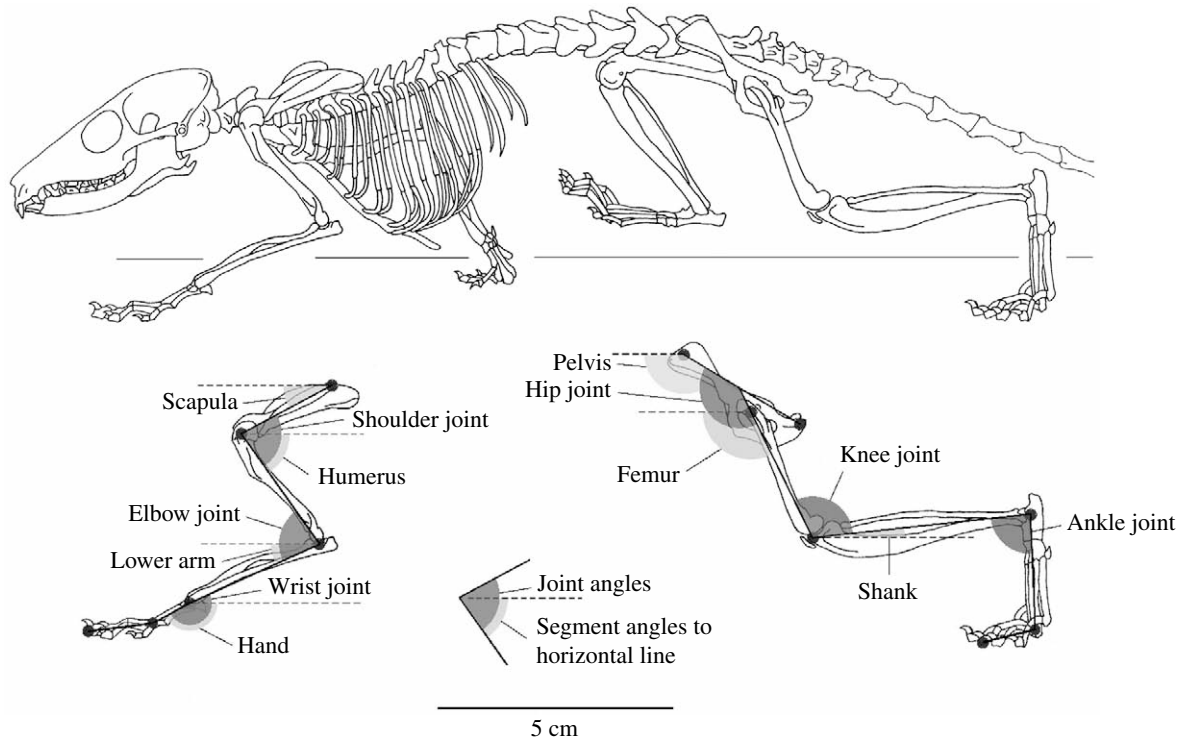


Fig. 2. Examples of skeletal landmarks used and angles calculated in an adult tree shrew (modified from Schilling and Fischer, 1999).

vectors for the calculation of metric and kinematic parameters. Locations of captured skeletal landmarks are illustrated in Fig. 2.

Metric parameters were calculated as vertical (e.g. height of fulcra) and horizontal (e.g. step length) distances. Segment angles were calculated from the horizontal, and joint angles were calculated on the flexion side of each joint (Fig. 2). Mean touch-down and lift-off angles, effective angular movements, maximum and minimum segment and joint angles, and maximum joint excursions were determined and compared among individuals (Table 2). Mean touch-down and lift-off angles of all cuis and all juvenile tree shrews were correlated with body mass and age. Adult tree shrews were excluded, because their exact age was unknown. The regression coefficient (r) and confidence intervals were calculated to determine the extent to which the slope differed from zero.

Segment and joint angles were projected onto the sagittal plane to calculate their contribution to step length. The contribution of joint angular movements to total step length was calculated by the 'overlay method' (for details, see Fischer and Lehmann, 1998; Fischer et al., 2002). The 'overlay method' takes into account that displacements of more proximal elements and vertical displacements of pivots during stance contribute to segment displacements. Calculations were based on mean values of selected, typical gait sequences; the stance and swing phases were normalized to the same period using linear interpolation.

Mean heights of the fore- and hindlimb pivots were calculated. The pivot of the forelimb was assumed to lie where the scapular spine meets the vertebral border of the scapula. In the hindlimb, the hip joint was assumed to be the fulcrum. In order to compare the limb excursions at touch-down and lift-off among different age stages, the horizontal distance between

Table 2. *Definitions of motion analysis and locomotor parameters*

Touch-down	Hard contact of foot at the beginning of stance
Lift-off	Last moment of ground contact at the end of stance
Stride (step cycle)	From the instance of one touch-down to the next touch-down of the same foot, including one stance and one swing phase
Protraction	Cranial displacement of a limb segment = cranial rotation (Fischer, 1994), flexion (English, 1978; Boczek-Funcke et al., 1996), anteversion
Retraction	Caudal displacements of a limb segment = caudal rotation (Fischer, 1994), extension (English, 1978; Boczek-Funcke et al., 1996), retroversion
Effective angular movement (°)	Absolute value of the difference between touch-down and lift-off angles
Amplitude (°)	Difference between maximum and minimum angles for stance and swing phase separately (maximum angular movement)

the position of the limb's fulcrum and the touch-down or lift-off point were expressed as a percentage of the height of the limb's fulcrum (relative limb protraction and retraction, respectively).

Error evaluation

Optical distortion due to parallax and aspect ratio were automatically corrected during frame-by-frame analysis. The accuracy of capturing skeletal landmarks is affected by the contrast of bones due to differences in thickness and calcification at different ages. The error of capturing skeletal landmarks was tested by repeatedly marking all landmarks in five different frames, five times, for the youngest animals and the adults of both species. Average standard deviations (S.D.) of the mean values of coordinates and angles indicate the error for marking landmarks. Error ranged between 0.1 mm and 1.4 mm for *x*- and *y*-coordinates, 0.3–9.9° for segment angles, and 1.1–10.6° for joint angles. Joint angle error is higher because the errors of adjacent segment angles may be cumulative in joint angles. No differences between fore- and hindlimb landmarks were found. Standard deviations were higher for younger animals with thinner bones than for older ones. Within limbs, more gracile limb elements, such as phalanges and scapular fulcra, are more prone to digitising errors than robust long bones (e.g. humerus or femur).

Results

Altogether, 1412 step cycles of the different age stages of both mammalian species were analysed in 21 000 X-ray frames for the present study. Fore- and hindlimb kinematics were studied in 664 step cycles of 13 age stages of tree shrew and 748 steps of 15 stages of cui during symmetrical gaits (Table 1).

General limb performance in juveniles was comparable to that of adults even during the first steps. Limbs were always arranged in the typical zigzag limb configuration. Limb segment and joint movements showed the same trajectories as in adults. Major changes in limb position during postnatal development occurred, and were especially noticeable at the end of stance phase.

Fulcra and limb position

In all animals, independent of age, fore- and hindlimb pivots (scapular fulcrum and hip joint) were at the same height above the ground. During locomotion, both pivots were held at nearly the same level; no drastic vertical fluctuations occurred. During development, the vertical

distance between ground and limb pivots increased by one third in both species (tree shrew: P14 34 mm, adult 47 mm; cui: P0 32 mm, adult 45 mm).

In order to compare limb's pro- and retraction between individuals of different body size at touch-down and lift-off, the limb pivots were scaled to the same vertical distance (100%) and the position of touch-down or lift-off was expressed as a

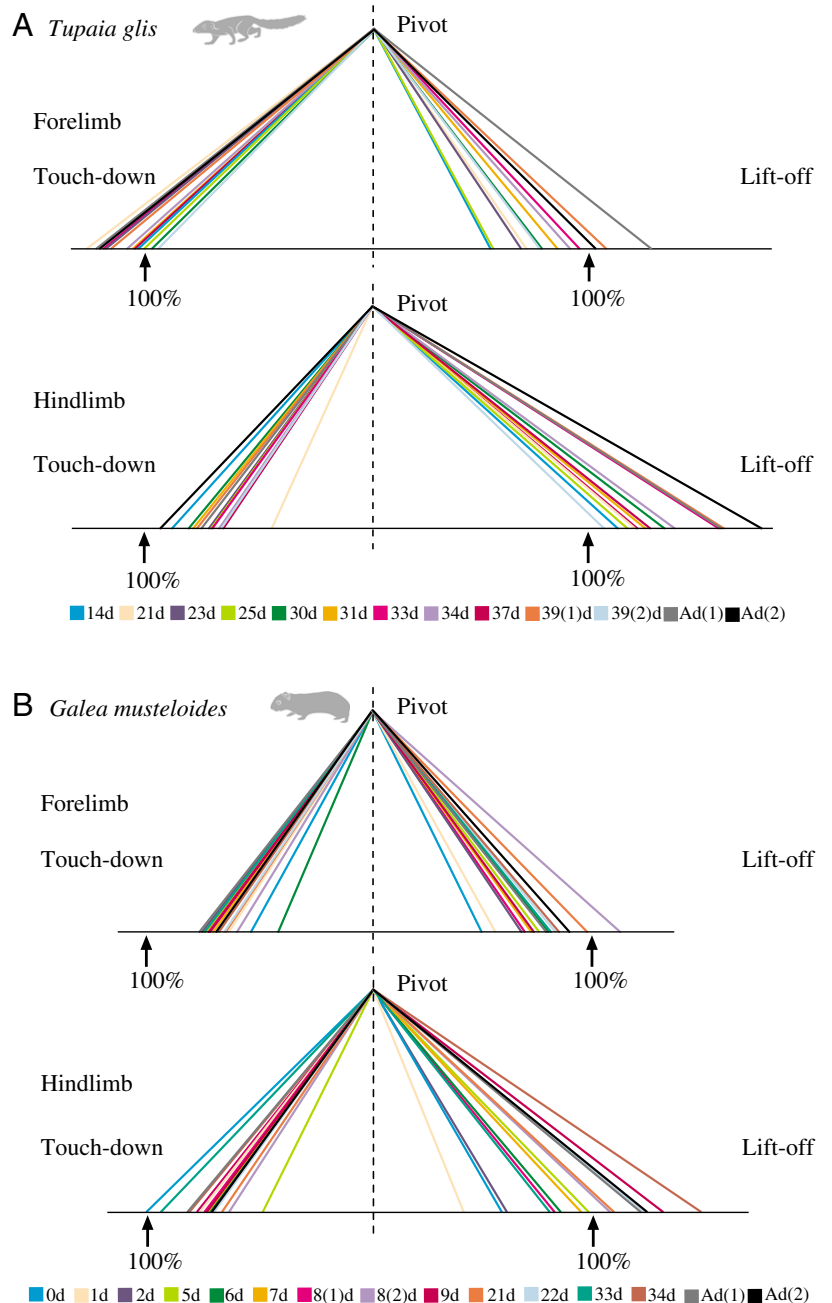


Fig. 3. Mean horizontal displacement of the limbs of (A) *Tupaia glis* and (B) *Galea musteloides* during stance phase. Pivot heights were scaled to the same vertical distance (=100%). Arrows indicate one-pivot-height distance away from the horizontal projection of the pivot's perpendicular. Note the caudal displacement of lift-off position with increasing age and the more consistent touch-down position. Animals are colour coded according to age (see Table 1).

Table 3. Kinematic data of the forelimb of all individuals of both species

Joint	Age (days)	Touch-down	Lift-off	Stance		Swing	
				Min	Max	Min	Max
<i>Scapula</i>							
<i>Tupaia glis</i>							
	14	48±9 (15)	87±8 (17)	46±10 (8)	98±4 (8)	39±8 (11)	92±9 (11)
	21	41±6 (21)	86±7 (23)	37±7 (18)	100±6 (18)	33±6 (17)	91±8 (17)
	23	47±6 (23)	86±7 (23)	43±6 (20)	98±3 (20)	39±5 (20)	93±7 (20)
	25	47±5 (24)	84±6 (27)	45±4 (16)	95±5 (16)	44±6 (18)	84±7 (18)
	30	43±6 (17)	94±8 (18)	41±5 (16)	103±7 (16)	36±3 (16)	97±9 (16)
	31	44±5 (18)	88±6 (20)	43±4 (18)	95±5 (18)	40±4 (18)	89±5 (18)
	33	46±6 (26)	89±5 (27)	43±6 (26)	95±3 (26)	40±5 (25)	91±3 (25)
	34	48±5 (23)	87±6 (25)	47±5 (22)	95±3 (22)	44±5 (24)	87±5 (24)
	37	47±5 (39)	95±8 (43)	46±5 (39)	104±7 (39)	43±4 (39)	96±7 (39)
	39(1)	45±6 (30)	92±6 (34)	43±5 (26)	97±4 (26)	41±5 (28)	92±6 (28)
	39(2)	52±7 (32)	89±6 (36)	49±6 (32)	95±4 (32)	44±6 (30)	92±7 (30)
	Ad(1)	34±3 (43)	93±4 (43)	33±2 (38)	95±3 (38)	32±3 (37)	94±4 (37)
	Ad(2)	41±4 (64)	91±4 (63)	39±3 (55)	94±3 (55)	38±3 (57)	92±4 (57)
<i>Galea musteloides</i>							
	0	52±9 (15)	81±7 (18)	45±8 (13)	89±5 (13)	41±7 (15)	83±6 (15)
	1	49±5 (31)	85±4 (30)	46±4 (28)	89±3 (28)	44±5 (29)	86±3 (29)
	2	42±5 (22)	79±7 (23)	38±5 (22)	88±4 (22)	35±6 (22)	81±6 (22)
	5	44±5 (28)	85±6 (27)	42±6 (25)	90±4 (25)	36±4 (24)	86±6 (24)
	6	47±6 (24)	86±4 (26)	46±5 (24)	89±3 (24)	35±3 (24)	88±3 (24)
	7	46±6 (31)	83±5 (29)	43±5 (25)	90±3 (25)	41±6 (27)	85±4 (27)
	8(1)	45±6 (20)	79±9 (22)	43±4 (20)	88±4 (20)	39±4 (21)	79±9 (21)
	8(2)	46±6 (31)	83±6 (32)	45±7 (30)	88±4 (30)	38±6 (30)	86±4 (30)
	9	45±5 (28)	82±5 (26)	43±4 (24)	87±2 (24)	37±3 (24)	82±5 (24)
	21	42±6 (37)	84±7 (34)	41±6 (31)	91±5 (31)	33±4 (32)	86±7 (32)
	22	39±4 (32)	86±4 (31)	38±4 (29)	89±3 (29)	31±3 (28)	87±3 (28)
	33	38±5 (27)	87±5 (26)	38±5 (24)	93±4 (24)	31±4 (21)	88±6 (21)
	34	41±4 (32)	81±4 (32)	41±4 (30)	88±2 (30)	33±3 (30)	82±3 (30)
	Ad(1)	41±3 (30)	84±3 (30)	40±2 (28)	92±3 (28)	35±3 (28)	84±3 (28)
	Ad(2)	46±5 (32)	88±5 (34)	45±3 (29)	93±2 (29)	38±3 (30)	89±5 (30)
<i>Humerus</i>							
<i>Tupaia glis</i>							
	14	77±10 (15)	-29±13 (17)	-35±7 (8)	76±10 (8)	-38±8 (11)	80±11 (11)
	21	83±11 (21)	-28±6 (23)	-29±6 (18)	84±10 (18)	-34±6 (17)	95±11 (17)
	23	80±16 (23)	-30±8 (23)	-32±6 (20)	79±15 (20)	-41±6 (20)	87±17 (20)
	25	78±12 (24)	-16±6 (27)	-19±4 (16)	76±13 (16)	-24±7 (18)	83±11 (18)
	30	89±7 (17)	-11±6 (18)	-12±6 (16)	98±7 (16)	-20±7 (16)	104±10 (16)
	31	82±11 (18)	-10±6 (20)	-12±5 (18)	82±10 (18)	-23±4 (18)	95±13 (18)
	33	92±9 (26)	-21±6 (27)	-23±6 (26)	92±9 (26)	-27±3 (25)	100±10 (25)
	34	76±11 (23)	-20±6 (25)	-22±5 (22)	77±11 (22)	-30±5 (24)	86±13 (24)
	37	85±10 (39)	-25±6 (43)	-27±5 (39)	85±10 (39)	-32±5 (39)	98±7 (39)
	39(1)	77±11 (30)	-17±8 (34)	-22±5 (26)	77±9 (26)	-32±7 (28)	92±11 (28)
	39(2)	69±14 (32)	-30±10 (34)	-31±10 (32)	69±14 (32)	-39±8 (30)	77±15 (30)
	Ad(1)	83±8 (43)	-5±3 (43)	-14±5 (38)	83±8 (38)	-18±4 (37)	99±6 (37)
	Ad(2)	82±10 (64)	-17±4 (63)	-21±4 (55)	82±11 (55)	-29±5 (57)	97±8 (57)
<i>Galea musteloides</i>							
	0	53±15 (15)	-11±9 (19)	-11±10 (14)	55±13 (14)	-13±9 (15)	59±13 (15)
	1	44±9 (31)	-17±7 (30)	-19±6 (28)	46±5 (28)	-26±7 (29)	48±10 (29)
	2	35±5 (22)	-31±6 (23)	-37±5 (22)	36±4 (22)	-35±5 (22)	41±7 (22)
	5	36±9 (28)	-25±6 (27)	-27±5 (25)	35±8 (25)	-32±5 (24)	53±8 (24)
	6	37±7 (24)	-13±8 (26)	-15±6 (24)	37±6 (24)	-17±4 (24)	65±7 (24)
	7	37±7 (31)	-24±7 (29)	-30±3 (25)	37±6 (25)	-31±5 (27)	45±8 (27)
	8(1)	30±5 (20)	-32±7 (22)	-35±6 (20)	31±5 (20)	-35±7 (21)	42±6 (21)

Table 3. Continued

Joint	Age (days)	Touch-down	Lift-off	Stance		Swing	
				Min	Max	Min	Max
Humerus							
<i>Galea musteloides</i>							
	8(2)	46±7 (31)	-16±6 (32)	-18±4 (30)	47±7 (30)	-22±4 (30)	60±7 (30)
	9	40±5 (28)	-26±3 (26)	-28±2 (24)	40±5 (24)	-29±2 (24)	51±4 (24)
	21	41±12 (37)	-13±9 (34)	-21±8 (21)	41±12 (31)	-25±7 (32)	57±10 (32)
	22	50±8 (32)	-8±8 (31)	-13±5 (29)	50±8 (29)	-16±6 (28)	62±5 (28)
	33	39±8 (27)	-27±6 (26)	-29±4 (24)	38±8 (24)	-31±4 (21)	50±8 (21)
	34	41±6 (32)	-19±5 (32)	-22±4 (30)	41±6 (30)	-24±4 (30)	58±5 (30)
	Ad(1)	43±6 (30)	-26±4 (30)	-27±4 (28)	43±6 (28)	-30±3 (28)	53±5 (28)
	Ad(2)	43±8 (32)	-14±11 (34)	-21±9 (29)	44±7 (29)	-19±8 (30)	57±4 (30)
Lower arm							
<i>Tupaia glis</i>							
	14	9±6 (15)	105±12 (17)	6±3 (8)	115±7 (8)	2±6 (11)	104±14 (11)
	21	12±4 (21)	106±13 (23)	11±4 (18)	118±11 (18)	-1±4 (17)	108±12 (17)
	23	14±3 (23)	106±13 (23)	13±3 (20)	117±8 (20)	-3±4 (20)	107±12 (20)
	25	23±5 (24)	117±13 (27)	23±3 (16)	124±9 (16)	9±5 (18)	120±11 (18)
	30	31±6 (17)	121±12 (18)	31±6 (16)	129±11 (16)	6±6 (16)	121±12 (16)
	31	18±5 (18)	121±11 (19)	18±5 (17)	127±9 (17)	-3±5 (17)	122±10 (17)
	33	16±3 (26)	121±6 (27)	15±3 (26)	132±4 (26)	0±4 (25)	122±6 (25)
	34	15±4 (23)	121±13 (25)	15±4 (22)	128±10 (22)	4±3 (24)	122±12 (24)
	37	14±5 (39)	123±8 (43)	13±5 (39)	129±9 (39)	-4±6 (39)	123±8 (39)
	39(1)	16±5 (30)	135±11 (34)	16±5 (26)	139±9 (26)	-1±5 (28)	134±10 (28)
	39(2)	21±7 (32)	116±7 (36)	20±7 (32)	121±7 (32)	6±5 (30)	117±8 (30)
	Ad(1)	10±6 (43)	148±6 (43)	10±6 (38)	149±5 (38)	-1±4 (37)	149±6 (37)
	Ad(2)	9±4 (64)	133±9 (63)	8±4 (55)	135±8 (55)	-2±3 (57)	133±9 (57)
<i>Galea musteloides</i>							
	0	37±10 (16)	98±12 (20)	37±10 (15)	105±9 (15)	13±4 (15)	98±14 (15)
	1	29±6 (31)	107±7 (30)	29±6 (28)	111±4 (28)	15±5 (29)	108±8 (29)
	2	26±5 (22)	103±6 (23)	26±5 (22)	114±5 (22)	13±3 (22)	103±7 (22)
	5	31±7 (28)	118±9 (27)	31±7 (25)	120±5 (25)	7±4 (24)	119±9 (24)
	6	45±5 (24)	123±7 (26)	45±5 (24)	128±6 (24)	10±6 (24)	124±6 (24)
	7	26±6 (31)	119±7 (29)	26±7 (25)	123±5 (25)	9±4 (27)	120±6 (27)
	8(1)	29±5 (20)	105±9 (22)	29±5 (20)	116±5 (20)	11±4 (21)	106±9 (21)
	8(2)	35±4 (31)	111±7 (32)	35±4 (30)	117±5 (30)	11±3 (30)	112±7 (30)
	9	24±4 (28)	110±6 (26)	25±3 (24)	116±4 (24)	6±3 (24)	110±6 (24)
	21	36±7 (37)	129±13 (34)	36±8 (31)	135±9 (31)	9±4 (32)	129±13 (32)
	22	41±5 (32)	125±10 (31)	41±5 (29)	132±7 (29)	17±5 (28)	126±10 (28)
	33	31±5 (27)	118±15 (26)	31±5 (24)	128±7 (24)	4±4 (21)	117±15 (21)
	34	30±4 (32)	125±6 (32)	30±4 (30)	129±6 (30)	4±3 (30)	125±6 (30)
	Ad(1)	26±5 (30)	119±8 (30)	26±5 (28)	126±6 (28)	3±3 (28)	119±8 (28)
	Ad(2)	31±10 (32)	130±10 (34)	30±9 (29)	136±5 (29)	8±6 (30)	130±11 (30)
Hand							
<i>Tupaia glis</i>							
	14	6±4 (11)	101±32 (17)	1±1 (5)	103±35 (5)	-4±5 (7)	139±19 (7)
	21	9±5 (18)	131±20 (23)	2±2 (15)	135±12 (15)	-1±5 (14)	152±11 (14)
	23	10±5 (23)	139±8 (23)	3±3 (20)	137±8 (20)	1±1 (20)	159±10 (20)
	25	9±6 (19)	129±15 (27)	4±3 (14)	131±15 (14)	7±10 (15)	157±10 (15)
	30	9±4 (17)	149±12 (16)	5±2 (14)	152±9 (14)	2±3 (15)	166±9 (15)
	31	12±3 (18)	140±15 (19)	4±2 (17)	142±12 (17)	2±2 (17)	167±4 (17)
	33	8±5 (16)	136±15 (23)	0±0 (16)	139±13 (16)	1±4 (16)	160±6 (16)
	34	12±4 (23)	141±12 (25)	5±3 (22)	140±12 (22)	2±2 (24)	173±8 (24)
	37	9±3 (24)	140±14 (43)	4±2 (24)	144±13 (24)	2±1 (23)	170±8 (23)
	39(1)	7±4 (26)	153±10 (33)	4±2 (25)	154±11 (25)	2±2 (24)	172±7 (24)

Table 3. *Continued*

Joint	Age (days)	Touch-down	Lift-off	Stance		Swing	
				Min	Max	Min	Max
Hand							
<i>Tupaia glis</i>							
	39(2)	11±7 (31)	134±15 (36)	6±4 (31)	133±15 (31)	3±6 (29)	156±8 (29)
	Ad(1)	10±4 (43)	165±15 (40)	4±4 (38)	165±15 (38)	1±2 (33)	185±11 (33)
	Ad(2)	14±4 (63)	151±11 (61)	9±2 (54)	151±11 (54)	-5±7 (54)	175±7 (54)
<i>Galea musteloides</i>							
	0	44±11 (14)	118±21 (19)	26±5 (13)	121±19 (13)	18±7 (10)	143±18 (10)
	1	32±7 (31)	126±11 (30)	27±6 (28)	126±11 (28)	19±9 (29)	155±7 (29)
	2	33±5 (22)	154±13 (23)	28±6 (22)	155±12 (22)	18±5 (22)	164±8 (22)
	5	27±4 (28)	134±11 (27)	25±4 (25)	135±11 (25)	9±6 (24)	168±6 (24)
	6	39±8 (23)	141±13 (26)	29±5 (23)	142±13 (23)	25±11 (10)	166±8 (10)
	7	31±6 (31)	140±13 (29)	27±4 (25)	139±11 (25)	13±9 (27)	175±4 (27)
	8(1)	24±5 (17)	154±13 (22)	22±5 (17)	157±13 (17)	14±12 (19)	172±7 (19)
	8(2)	29±9 (31)	143±9 (32)	20±7 (30)	142±9 (30)	13±6 (30)	163±6 (30)
	9	29±3 (28)	142±11 (26)	28±4 (24)	141±11 (24)	9±4 (24)	174±4 (24)
	21	28±7 (37)	156±12 (34)	23±5 (31)	156±12 (31)	9±6 (32)	174±6 (32)
	22	31±5 (32)	148±10 (31)	27±4 (29)	148±9 (29)	15±6 (28)	174±4 (28)
	33	25±8 (27)	147±10 (26)	16±5 (24)	147±11 (24)	7±6 (21)	169±10 (21)
	34	27±5 (32)	144±13 (32)	25±4 (30)	144±12 (30)	4±4 (30)	173±6 (30)
	Ad(1)	24±5 (30)	145±13 (30)	19±3 (28)	147±11 (28)	6±4 (28)	175±5 (28)
	Ad(2)	28±5 (32)	156±11 (34)	21±5 (29)	156±12 (29)	9±5 (28)	178±2 (28)

Values are means ± s.d. (N =number of steps) of touch-down and lift-off angles as well as minimum (Min) and maximum (Max) angles during stance and swing phase.

Effective and maximum angular movements result from the differences of touch-down and lift-off angles and of minimum and maximum angles during stance or swing, respectively.

For further abbreviations, see Table 1.

percentage of the pivot's height (Fig. 3). In relation to the height of forelimb pivots, the horizontal distances between the limb pivot and the point of touch-down or lift-off were comparable in adults of both species (Fig. 3). In the tree shrew, this distance exceeded the height of the forelimb pivot by about 19%, resulting in a relative forelimb protraction of 119%, whereas relative limb protraction was much smaller in the cui (79%). Even in the youngest tree shrew, relative limb protraction at touch-down was higher (107%) than in all cuis under study. The position of forelimb touch-down was independent of body mass or age in both species and ranged between 101–126% in tree shrew and 43–78% in cui. No major changes in limb excursions at touch-down occurred during development. However, the horizontal distance between the scapular fulcrum and lift-off position doubled during development in both species (tree shrew: P14 53%, adult(1) 125%, adult(2) 100%; cui: P0 49%, adult(1) 78%, adult(2) 89%).

Independent of age and species, the horizontal distance between touch-down and hip joint position was less than the height of the hip joint. Distances ranged from 46–96% in tree shrew and 50–102% in cui. As in the forelimb, no changes in relative limb protraction at touch-down occurred during postnatal development; touch-down position was not correlated with age or mass. Lift-off position was significantly correlated with body mass in both species. In the course of

development of the cui, the horizontal distance between the hip joint and point of lift-off doubled (P0: 58%, adult(1) 121%, adult(2) 124%), while in tree shrew, this distance increased by 50% (P14 111%, adult(1) 158%, adult(2) 177%).

Segment and limb joint performance

In general, segment and joint movements started at the end of one step phase and continued into the next phase (for details of timing, see Schilling and Fischer, 1999). Therefore, the onset of protraction and retraction were not strictly coupled to touch-down and lift-off events. Timing of segment and limb joint movement was comparable to that in adults from the first steps of the youngest animals.

Scapula

Scapular movements were composed of rotational and translational components. Vertical and horizontal translations of the shoulder blade were ignored in this study because of technical limitations of the resolution of cinevideography. The scapular spine was used to indicate the orientation of the shoulder blade. Retraction of the shoulder blade started shortly before touch-down. Mean touch-down angles were similar in the adults of both species (Table 3). During stance phase, the shoulder blade rotated caudally to reach a maximum angle of 92–95° in both species. The scapula was already protracted at

lift-off, and therefore, mean lift-off angles were smaller than maximal excursions. During swing phase, the shoulder blade rotated cranially and reached a minimum angle of 32–38° in both species just before touch-down.

Mean touch-down angles of the juveniles were higher than those of adults in both species, but were significantly correlated with age and body mass only in *cuis* ($r=0.54$ and 0.51 , respectively; $P\leq 0.05$). Mean lift-off angles increased with age in tree shrews ($r=0.59$, $P\leq 0.05$) and with body mass in *cuis* ($r=0.50$, $P\leq 0.05$). The more protracted touch-down position of the scapula combined with the decreased caudal rotation at the end of stance phase resulted in lower effective angular movements in younger animals. Whereas the minimum angle during stance phase and touch-down angle were the same in adults, the minimum angle of stance was lower than touch-down angle until the age of P25 in tree shrews, as well as in the underweight individual P39(2), and until age P5 in *cuis*. Thus, the scapula was displaced cranially under load after touch-down in juveniles but was held at a constant position in the older animals.

Humerus

At touch-down, the humerus was held in a nearly vertical position in adult tree shrews and much more retracted in adult *cuis* (Table 3). During stance phase, the humerus rotated caudally, crossed its horizontal position and reached its minimum angle. Minimum angles in the adult *cuis* were slightly lower than in adult tree shrews. Because of synchronous extensions of shoulder and elbow joints at the end of stance, the humerus was rotated slightly cranially until and after lift-off, and therefore minimum values of swing were lower than lift-off angles. The humeral angle reached its minimum of swing phase within the first third of swing phase. The maximum angle of swing was much higher in the adult tree shrews and crossed the vertical line, but was much more inclined caudally in the adult *cuis* and never reached a vertical orientation. Because of the greater cranial excursion of the humerus, effective angular movement and amplitudes were greater in adult tree shrews than in adult *cuis*.

Although no significant changes in mean touch-down or lift-off angle were observed during postnatal development of the *cui*, mean lift-off angle of the humerus was correlated with body mass in the tree shrew ($r=0.78$, $P\leq 0.01$). In younger individuals, humerus was rotated beyond the horizontal position. Nevertheless, the humerus was rotated the same amount dorsally at lift-off in each age stage. Adult values of mean lift-off angles were observed for individuals larger than 121.0 g (P25) in the tree shrew. Mean touch-down angle did not change during ontogeny in tree shrews. The underweight tree shrew P39(2) was better classified with younger animals of comparable body mass. Because of the smaller angle at lift-off and the unchanged angle at touch-down, effective angular movement in juveniles exceeded those of adult tree shrews.

Lower arm

Mean minimum angles of the lower arm at the end of swing

phase were -1° and -2° in adult tree shrews and 3° and 8° in adult *cuis*, indicating a nearly horizontal position (Table 3). Retraction of the lower arm had already begun at touch-down. Therefore, mean touch-down angle was higher than the minimum angle of swing phase. Maximum angular excursion was reached at the end of stance phase, and slightly higher values were observed in adult tree shrews than in adult *cuis*. Mean lift-off angles were lower than maximum excursions, because protraction began before lift-off. Effective angular movements were higher in adult tree shrews than in adult *cuis* because of lower values at touch-down and higher values at lift-off.

In both species, changes in lift-off position of the lower arm were observed, but no changes in the touch-down position were evident during ontogeny. Lower arm angle at lift-off was correlated with age and body mass in the *cui* ($r=0.66$ and 0.67 , respectively; $P\leq 0.01$), but lift-off angle was more correlated with age than with body mass in the tree shrew ($r=0.83$, $P\leq 0.001$ and 0.73 , $P\leq 0.01$, respectively). Higher effective angular movements with increasing age or body mass were caused by increased angles at lift-off. Angles of juvenile *cuis* older than P5 were equivalent to those of adults. As in the humerus, all data from the underweight tree shrew P39(2) were comparable to those of younger individuals of the same body mass. Mean lift-off angle of the other tree shrew of the same age was not significantly different from adult values. Minimum angle during stance and angle at touch-down were similar in all age stages of both species, such that no cranial displacement under loading was observed.

Hand

Carpus and metacarpus were considered together as one segment. With a mean touch-down angle of 10° and 14° in tree shrews, the hand was a bit more declined in adult tree shrews than in adult *cuis* (24° and 28°) (Table 3). During stance phase, the palm was lifted from the ground into a digitigrade position and reached its maximum angle of retraction at lift-off. After lift-off, caudal rotation continued until the hand reached its maximum swing angle of 175 – 185° in adults of both species. The subsequent protraction ended when the hand attained minimal cranial rotation during swing phase. The hand crossed the horizontal in adult tree shrews but never reached the horizontal in adult *cuis*.

During postnatal development, no significant changes in the touch-down position of the hand were observed in the tree shrew, while mean touch-down angles decreased during development in the *cui* with age and body mass ($r=0.55$ and 0.49 , respectively; $P\leq 0.05$). The angle at lift-off increased with increasing age and body mass in tree shrews ($r=0.74$ and 0.73 , respectively; $P\leq 0.01$) and increasing age in *cuis* ($r=0.49$, $P\leq 0.05$). Mean angles at touch-down and at lift-off of the normal weight juvenile tree shrew P39(1) were similar to those of adults, while, these values of underweight individual of the same age P39(2) were comparable to younger animals of the same mass.

Shoulder joint

Because of the higher protraction of humerus at the beginning of stance, maximum extension of the shoulder joint before touch-down in adult tree shrews (134° and 138°, mean angles for each individual) exceeded the values of adult cuis

(91° and 99°; Fig. 4A,B). This was also reflected in larger mean touch-down angles in adult tree shrews than in adult cuis (tree shrew, 118° and 122°; cui, 84° and 89°). Flexion of the shoulder joint started before touch-down and continued during stance phase until the minimum value was reached as the hand

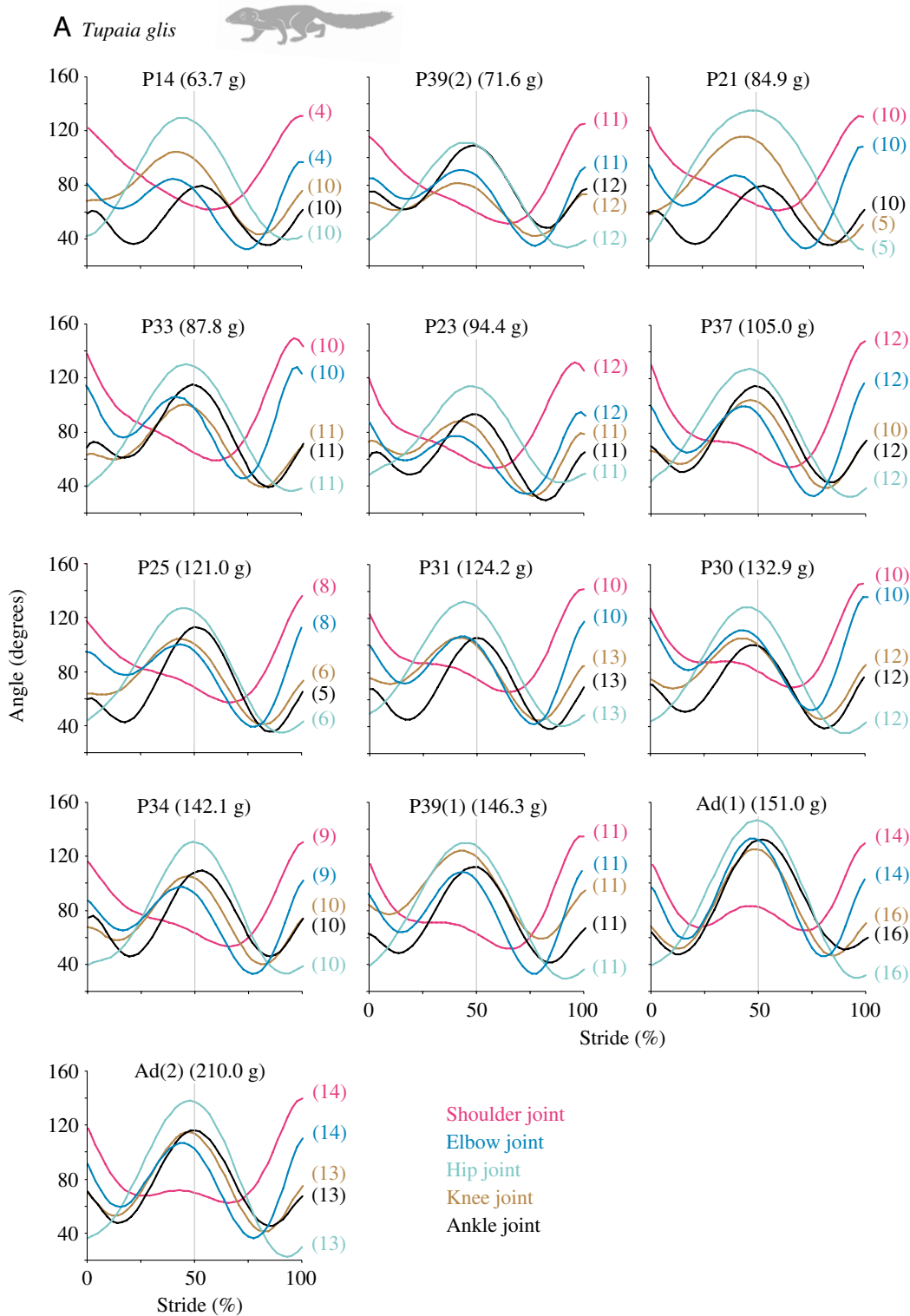


Fig. 4A.

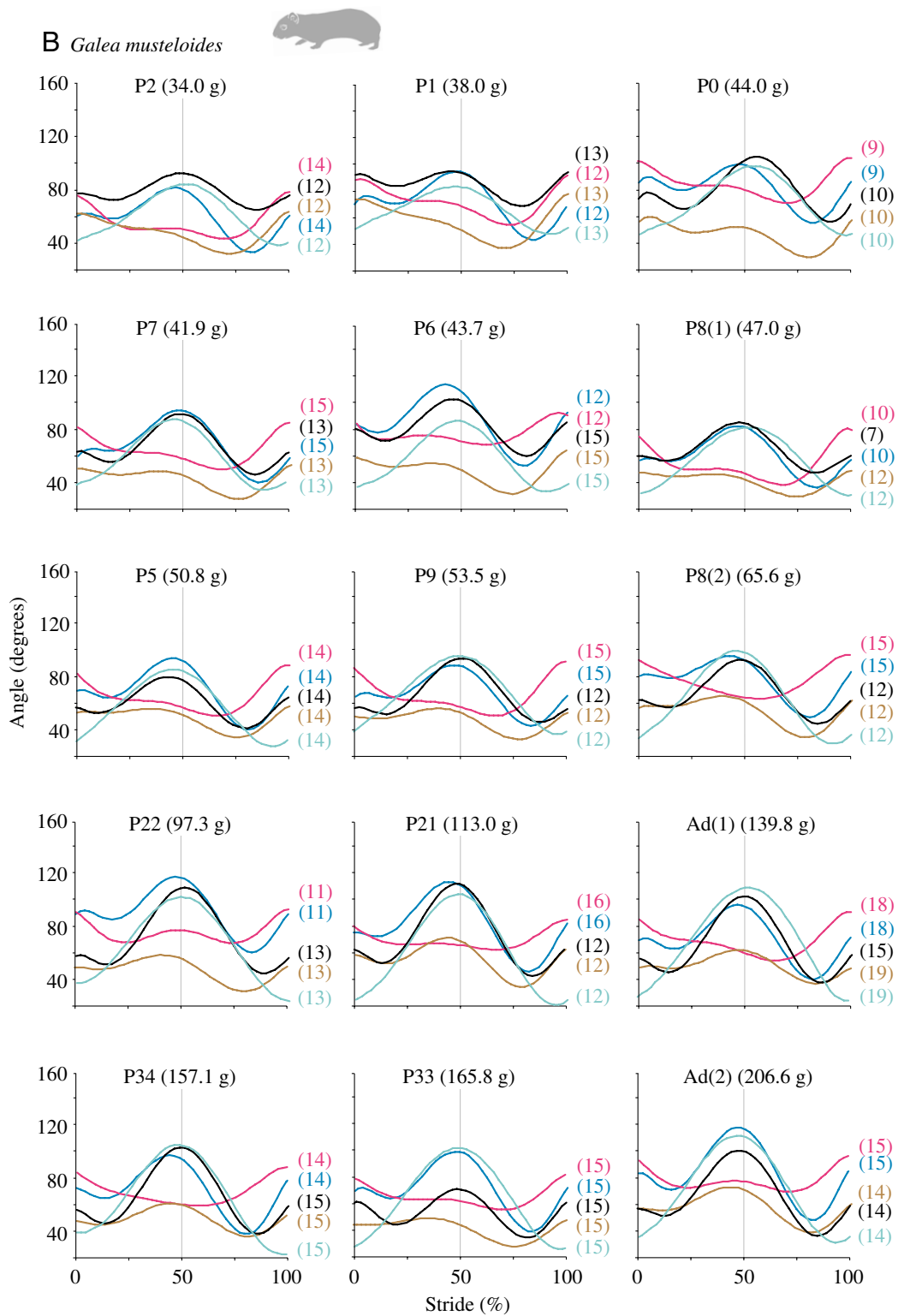


Fig. 4. Mean angular movement of the shoulder, elbow, hip, knee and ankle joint over one step cycle of all individuals of (A) *Tupaia glis* and (B) *Galea musteloides*, sorted by body mass. Numbers in parentheses indicate number of steps used. Stance and swing duration were scaled to the same length by linear interpolation: 0% and 100%=touch-down; 50%=lift-off. Note how the monophasic angular movement in the shoulder joint in juvenile tree shrews becomes more and more biphasic during development. The shoulder joint movement of the underweight tree shrew juvenile P39(2) is similar to that of younger individuals. Despite this, the angular movement in the precocial cui is more or less biphasic from birth. Furthermore, note the increasing synchronization of maximum joint extension during stance.

passed the below the shoulder joint. Both species exhibited similar mean minimum angle (56° to 67°). At the end of stance, the shoulder joint extended a second time, while the elbow joint extended and the humerus was rotated cranially. At lift-off, mean shoulder joint angles reached 88° and 75° in adult tree shrews and 58° and 75° in adult cuis. After lift-off, the shoulder joint was flexed until its minimum during swing phase (47° to 58°) and the subsequent extension continued until the end of swing phase. Because of greater extension at the beginning of stance and similar lift-off angles, adult tree shrews showed greater effective angular movements and amplitudes than adult cuis.

As in the humerus, no changes in mean touch-down or lift-off position occurred with increasing age or body mass during the development of the cui. In the tree shrew, touch-down position was not significantly correlated with body mass or age, but mean lift-off angle increased with increasing body mass ($r=0.76$, $P\leq 0.01$). By the age that young tree shrews leave the nest P39(1), shoulder joint values were comparable to those of adults. Mean values of the underweight tree shrew P39(2) were similar to those of younger animals with the same body mass. Because of the smaller lift-off angle of the shoulder blade and the more caudally rotated humerus in the tree shrew, mean lift-off angle was smaller in younger animals than in adults. The shoulder joint was more flexed in younger stages at lift-off. The smaller angle at lift-off and unchanged touch-down angles resulted in higher effective angular movements in tree shrew juveniles than in adults. Values of juvenile tree shrews were comparable to those of adults by age P30. Higher amplitude shoulder joint angles during stance and swing phase in juvenile tree shrews resulted from stronger flexion and extension of the shoulder joint. Because of similar touch-down and lift-off angles and comparable minimum and maximum values of young and old cuis, effective angular movement and amplitudes were nearly constant during development.

Mean shoulder joint angle in adult tree shrews plotted against step cycle shows biphasic joint movement including two flexions and two extensions (Fig. 4A,B). In the altricial tree shrew juveniles, shoulder joint movement was monophasic, but the typical biphasic joint angle pattern developed as body mass increased. Notice that the angular movement of the under nourished juvenile P39(2) was comparable to those of younger animals of similar mass. During the development of precocial cuis, this biphasic joint movement varied, but no change during development was evident.

Elbow joint

At touch-down, the elbow joint was held at a right angle in adult tree shrews (92° and 90° ; Fig. 4A,B). The elbow was more flexed in adult cuis, with mean touch-down angles of 69° and 74° . During stance phase, the elbow was first flexed to a mean minimum angle of 58° to 65° in both species, as the hand passed below the fulcrum of the forelimb. Then the elbow joint underwent extension until reaching maximum values of 145° and 120° in adult tree shrews and 105° and 124° in adult cuis

at the end of stance. Flexion of the joint during swing phase began before lift-off and therefore mean lift-off angles (tree shrew, 143° and 116° ; cui, 93° and 117°) were less than maximum extensions. After minimum flexion during swing phase (26 – 38°), the elbow joint extended until its maximum was reached at the end of swing phase (tree shrew, 144° and 119° ; cui, 93° and 116°). The following flexion phase lasted until the middle of the subsequent stance phase.

Mean touch-down angle of the elbow joint was not correlated with body mass or age in either species, i.e. no developmental changes in elbow joint angle occurred during touch-down. Despite this, significant changes in mean lift-off position were found. Whereas mean lift-off angles were more correlated with body mass than with age in the tree shrew ($r=0.84$, $P\leq 0.001$ and $r=0.65$, $P\leq 0.05$, respectively), mean lift-off angles were correlated equally well with body mass and age in the cui ($r=0.55$ and 0.49 , respectively; $P\leq 0.05$). The elbow joint was more flexed at lift-off in the youngest tree shrew individuals (body mass below 100 g) than in the youngest cui individuals (joint angle of about 90°). With increasing body mass, lift-off angles of juvenile tree shrews exceeded those of young cuis. At the age they left the nest, joint angles of tree shrews P39(1) were similar to those of adults. In cuis, there were no major changes in elbow joint angle at lift-off after the first week of life.

Wrist joint

At touch-down, the hand was simply a continuation of the lower arm in both species (wrist joint angle, 176° to 185°). The wrist joint was increasingly flexed from touch-down until mid-stance. The minimum angle reached was 117° and 129° in adult tree shrews and 129° and 132° in adult cuis. The wrist joint subsequently extended when the palm left the ground until the next swing phase. Mean lift-off angles were 198° in adult tree shrews and 206° in adult cuis. After maximum wrist extension during swing phase (tree shrew, 270° and 255° ; cui, 268° and 260°), the wrist joint flexed during the short swing time before touch-down. Mean minimum joint angle during swing phase was comparable between both species (169° to 173°).

Wrist angle at touch-down and lift-off did not change with increasing body mass or age. Due to comparable touch-down and lift-off angles as well as minimum and maximum excursions, the effective and maximum angular movements of juveniles and adults were similar.

Pelvis

Because of the rigid connection between the pelvis and sacrum, all observable 'pelvic movements' were the result of small, additive, intervertebral movements. During walking and trotting, 'pelvic movements' occur mainly around the dorsoventral and longitudinal axes of the pelvis (lateral bending and tilting, respectively; Jenkins and Camazine, 1977). Sagittal vertebral movements resulting in pelvic protraction and retraction are less pronounced during symmetrical gaits than during asymmetrical gaits. Lateral

Table 4. Kinematic data of the hindlimb of all individuals of both species

Bone	Age (days)	Touch-down	Lift-off	Stance		Swing	
				Min	Max	Min	Max
Pelvis							
<i>Tupaia glis</i>							
	14	157±5 (26)	161±6 (22)	151±3 (13)	168±4 (13)	155±5 (22)	167±5 (22)
	21	160±10 (21)	169±6 (9)	160±3 (6)	177±3 (6)	161±6 (9)	175±4 (9)
	23	159±6 (36)	164±5 (33)	151±5 (28)	170±3 (28)	155±6 (29)	169±4 (29)
	25	160±4 (36)	164±3 (24)	156±3 (21)	167±2 (21)	157±4 (22)	166±2 (22)
	30	160±6 (25)	166±5 (24)	155±5 (22)	170±4 (22)	157±6 (24)	168±4 (24)
	31	158±3 (19)	163±3 (21)	154±4 (19)	165±3 (19)	155±4 (19)	165±3 (19)
	33	159±4 (21)	163±3 (23)	155±3 (21)	168±2 (21)	156±4 (23)	168±3 (23)
	34	157±7 (43)	165±4 (46)	150±5 (43)	169±3 (43)	155±6 (43)	168±4 (43)
	37	166±5 (47)	169±6 (33)	158±5 (29)	174±5 (29)	161±6 (31)	173±6 (31)
	39(1)	161±7 (42)	166±4 (37)	154±8 (33)	170±3 (33)	157±8 (32)	169±4 (32)
	39(2)	159±5 (41)	161±5 (36)	153±3 (3)5	167±4 (35)	155±4 (32)	165±4 (32)
	Ad(1)	161±5 (34)	164±5 (33)	157±5 (30)	170±4 (30)	157±5 (30)	168±5 (30)
	Ad(2)	161±4 (39)	163±3 (36)	158±4 (30)	168±3 (30)	158±5 (33)	168±4 (33)
<i>Galea musteloides</i>							
	0	130±9 (19)	135±8 (21)	122±5 (19)	144±8 (19)	127±7 (19)	143±8 (19)
	1	140±4 (30)	141±5 (31)	135±4 (28)	148±4 (28)	136±5 (29)	147±4 (29)
	2	148±5 (23)	152±4 (26)	144±5 (23)	160±3 (23)	146±5 (24)	160±3 (24)
	5	166±5 (25)	169±4 (28)	163±5 (25)	172±4 (25)	162±5 (22)	173±3 (22)
	6	146±6 (23)	149±6 (25)	139±9 (23)	155±5 (23)	140±9 (24)	156±4 (24)
	7	157±6 (27)	159±6 (20)	153±6 (18)	166±6 (18)	155±5 (18)	167±6 (18)
	8(1)	157±4 (20)	161±5 (23)	154±4 (20)	168±3 (20)	154±3 (23)	168±3 (23)
	8(2)	159±3 (31)	160±3 (31)	158±2 (29)	166±2 (29)	157±2 (29)	166±2 (29)
	9	158±3 (27)	158±4 (26)	155±3 (24)	166±2 (24)	155±3 (25)	166±2 (25)
	21	163±6 (24)	166±4 (30)	157±8 (20)	172±4 (20)	159±7 (20)	172±4 (20)
	22	154±6 (32)	156±5 (32)	150±5 (29)	163±6 (29)	151±6 (29)	163±6 (29)
	33	149±5 (24)	152±4 (24)	146±6 (22)	158±6 (22)	147±5 (22)	157±6 (22)
	34	159±3 (33)	160±3 (33)	156±4 (31)	167±4 (31)	157±4 (31)	167±4 (31)
	Ad(1)	152±2 (30)	157±5 (28)	149±2 (26)	166±2 (26)	150±2 (28)	166±2 (28)
	Ad(2)	158±4 (31)	159±4 (31)	155±4 (29)	165±4 (29)	155±4 (29)	165±4 (29)
Femur							
<i>Tupaia glis</i>							
	14	21±11 (26)	102±18 (22)	17±10 (13)	115±14 (13)	14±8 (22)	105±17 (22)
	21	21±12 (21)	119±13 (9)	20±7 (6)	127±12 (6)	14±13 (9)	122±11 (9)
	23	24±9 (36)	102±14 (33)	22±9 (28)	109±13 (28)	18±9 (29)	101±15 (29)
	25	20±8 (36)	103±13 (24)	20±6 (21)	109±8 (21)	13±8 (22)	103±14 (22)
	30	21±7 (25)	109±11 (24)	21±8 (22)	117±10 (22)	13±6 (24)	109±11 (24)
	31	23±4 (19)	108±4 (21)	23±4 (19)	115±4 (19)	14±3 (19)	108±4 (19)
	33	16±7 (21)	113±8 (23)	16±7 (21)	120±6 (21)	11±7 (23)	114±9 (23)
	34	15±9 (43)	112±8 (45)	14±9 (42)	116±8 (42)	7±6 (42)	112±9 (42)
	37	25±8 (47)	113±8 (33)	25±9 (29)	118±7 (29)	17±6 (31)	113±8 (31)
	39(1)	20±9 (42)	119±13 (37)	20±10 (33)	122±11 (33)	8±7 (32)	120±13 (32)
	39(2)	19±7 (41)	93±13 (36)	19±7 (35)	99±10 (35)	8±4 (32)	93±14 (32)
	Ad(1)	16±6 (34)	125±10 (33)	16±6 (30)	127±9 (30)	9±5 (30)	125±10 (30)
	Ad(2)	11±10 (39)	125±8 (36)	12±10 (30)	126±7 (30)	3±6 (33)	126±9 (33)
<i>Galea musteloides</i>							
	0	1±9 (19)	36±17 (21)	-3±9 (19)	50±15 (19)	-7±7 (19)	40±15 (19)
	1	15±6 (30)	47±7 (31)	12±5 (28)	52±5 (28)	6±5 (29)	48±6 (29)
	2	12±5 (23)	53±6 (26)	11±4 (23)	55±6 (23)	6±3 (24)	54±6 (24)
	5	24±11 (25)	77±10 (28)	24±11 (25)	81±8 (25)	10±7 (22)	79±9 (22)
	6	9±6 (23)	58±8 (25)	8±7 (23)	63±7 (23)	-1±6 (24)	59±7 (24)
	7	11±8 (27)	63±10 (20)	11±10 (18)	71±9 (18)	2±6 (18)	66±11 (18)
	8(1)	13±6 (20)	63±8 (23)	12±7 (20)	68±7 (20)	7±4 (23)	65±8 (23)

Table 4. *Continued*

Bone	Age (days)	Touch-down	Lift-off	Stance		Swing	
				Min	Max	Min	Max
Femur							
<i>Galea musteloides</i>							
	8(2)	23±7 (31)	81±9 (31)	22±7 (29)	86±6 (29)	9±4 (29)	82±10 (29)
	9	21±5 (27)	71±5 (26)	21±6 (24)	79±4 (24)	12±5 (25)	72±4 (25)
	21	11±8 (24)	88±11 (30)	11±8 (20)	90±8 (20)	3±5 (20)	87±10 (20)
	22	14±7 (32)	77±5 (32)	14±7 (29)	82±5 (29)	3±5 (29)	79±4 (29)
	33	3±9 (24)	73±15 (24)	2±10 (22)	76±14 (22)	-4±7 (22)	72±14 (22)
	34	11±6 (33)	85±5 (33)	11±6 (31)	87±4 (31)	2±3 (31)	86±5 (31)
	Ad(1)	5±4 (30)	81±6 (28)	5±4 (26)	84±5 (26)	0±3 (28)	81±6 (28)
	Ad(2)	23±8 (31)	91±7 (31)	23±7 (29)	94±7 (29)	8±7 (29)	86±7 (29)
Shank							
<i>Tupaia glis</i>							
	14	51±7 (26)	-9±8 (22)	-10±5 (13)	52±8 (13)	-19±8 (22)	53±7 (22)
	21	39±9 (21)	-4±9 (9)	-11±6 (6)	39±3 (6)	-32±7 (9)	41±11 (9)
	23	46±8 (36)	-6±8 (33)	-9±5 (28)	48±7 (28)	-30±6 (29)	50±10 (29)
	25	46±9 (36)	-3±6 (24)	-4±5 (21)	47±8 (21)	-13±5 (22)	51±9 (22)
	30	54±8 (25)	-4±7 (24)	-6±6 (22)	54±9 (22)	-20±4 (24)	59±8 (24)
	31	53±4 (19)	-3±4 (21)	-4±4 (19)	53±4 (19)	-19±4 (19)	59±5 (19)
	33	45±10 (21)	-7±5 (23)	-14±4 (21)	45±10 (21)	-26±5 (23)	49±10 (23)
	34	49±11 (43)	-3±9 (37)	-9±6 (34)	48±12 (34)	-24±6 (37)	56±9 (37)
	37	51±6 (47)	-2±4 (33)	-4±4 (29)	52±6 (29)	-17±6 (31)	57±7 (31)
	39(1)	47±10 (42)	-1±8 (35)	-9±6 (31)	46±11 (31)	-22±4 (30)	56±11 (30)
	39(2)	48±7 (41)	-9±6 (35)	-12±5 (34)	48±7 (34)	-21±5 (31)	55±6 (31)
	Ad(1)	49±7 (34)	-1±6 (33)	-11±5 (30)	48±7 (30)	-18±6 (30)	60±6 (30)
	Ad(2)	49±7 (39)	-6±7 (36)	-14±4 (30)	48±6 (30)	-24±5 (33)	59±6 (33)
<i>Galea musteloides</i>							
	0	63±8 (19)	3±8 (21)	-1±9 (19)	63±7 (19)	-2±8 (19)	64±6 (19)
	1	60±4 (30)	-3±5 (31)	-3±5 (28)	60±3 (28)	-6±5 (29)	62±4 (29)
	2	52±5 (23)	-11±5 (26)	-11±5 (23)	52±5 (23)	-13±5 (24)	56±5 (24)
	5	30±9 (25)	-22±4 (28)	-22±4 (25)	30±9 (25)	-28±4 (22)	39±7 (22)
	6	52±7 (23)	-9±5 (25)	-9±6 (23)	52±7 (23)	-14±6 (24)	58±7 (24)
	7	39±10 (27)	-20±7 (20)	-21±7 (18)	39±12 (18)	-26±7 (18)	47±8 (18)
	8(1)	35±7 (20)	-25±6 (23)	-26±6 (20)	35±7 (20)	-28±6 (23)	40±5 (23)
	8(2)	38±6 (31)	-21±3 (31)	-22±2 (29)	37±6 (29)	-26±3 (29)	44±5 (29)
	9	29±6 (27)	-25±4 (26)	-25±3 (24)	29±6 (24)	-30±2 (25)	38±6 (25)
	21	46±9 (24)	-19±7 (30)	-21±7 (20)	47±8 (20)	-29±4 (20)	54±6 (20)
	22	41±7 (32)	-20±6 (32)	-21±6 (29)	41±7 (29)	-27±6 (29)	50±6 (29)
	33	43±10 (24)	-29±4 (24)	-29±4 (22)	43±10 (22)	-32±5 (22)	50±9 (22)
	34	39±7 (33)	-24±4 (33)	-25±4 (31)	39±7 (31)	-30±4 (31)	49±5 (31)
	Ad(1)	45±6 (30)	-25±4 (28)	-25±4 (26)	44±6 (26)	-32±2 (28)	51±5 (28)
	Ad(2)	32±7 (31)	-22±3 (31)	-22±3 (29)	31±7 (29)	-27±5 (29)	51±6 (29)
Foot							
<i>Tupaia glis</i>							
	14	11±6 (26)	93±13 (22)	5±4 (13)	96±12 (13)	-4±6 (22)	97±14 (22)
	21	17±12 (20)	124±11 (5)	15±5 (4)	129±2 (4)	4±19 (5)	131±4 (5)
	23	12±5 (36)	117±9 (27)	11±4 (23)	117±10 (23)	-1±8 (24)	121±11 (24)
	25	13±6 (36)	122±13 (21)	12±6 (18)	120±11 (18)	4±10 (19)	129±9 (19)
	30	12±5 (25)	118±9 (24)	11±5 (20)	118±10 (20)	3±7 (24)	120±10 (24)
	31	10±4 (19)	121±6 (21)	10±4 (19)	121±6 (19)	-3±6 (19)	124±7 (19)
	33	24±7 (21)	133±6 (21)	24±7 (19)	134±5 (19)	13±7 (21)	135±7 (21)
	34	17±7 (43)	127±6 (28)	16±7 (27)	128±6 (27)	8±5 (28)	129±6 (28)
	37	13±7 (47)	123±7 (30)	14±8 (27)	123±7 (27)	4±8 (28)	125±7 (28)
	39(1)	11±5 (42)	133±10 (21)	10±5 (19)	132±10 (19)	0±7 (19)	137±7 (19)

Table 4. Continued

Bone	Age (days)	Touch-down	Lift-off	Stance		Swing	
				Min	Max	Min	Max
Foot							
<i>Tupaia glis</i>							
	39(2)	23±7 (41)	123±7 (28)	21±8 (27)	123±6 (27)	8±6 (25)	126±8 (25)
	Ad(1)	9±4 (34)	138±6 (32)	9±4 (29)	138±7 (29)	4±4 (30)	142±6 (30)
	Ad(2)	14±5 (39)	125±8 (36)	14±5 (30)	126±7 (30)	-1±6 (32)	134±6 (32)
<i>Galea musteloides</i>							
	0	15±10 (19)	95±19 (21)	11±9 (19)	97±18 (19)	7±7 (19)	96±19 (19)
	1	30±6 (30)	94±7 (30)	29±6 (27)	95±7 (27)	22±5 (29)	94±7 (29)
	2	25±7 (23)	100±8 (26)	24±7 (23)	101±7 (23)	20±5 (24)	101±8 (24)
	5	26±7 (25)	114±12 (28)	26±7 (25)	114±12 (25)	19±5 (22)	116±13 (22)
	6	29±9 (23)	116±10 (25)	28±8 (23)	117±11 (23)	22±7 (24)	117±10 (24)
	7	20±6 (27)	110±10 (18)	20±6 (16)	112±9 (16)	13±5 (15)	112±9 (15)
	8(1)	22±5 (20)	130±13 (10)	20±4 (8)	106±15 (8)	17±4 (10)	103±13 (10)
	8(2)	23±6 (31)	119±6 (31)	23±6 (29)	119±6 (29)	13±4 (29)	121±6 (29)
	9	26±3 (27)	120±4 (26)	26±3 (24)	120±4 (24)	18±3 (25)	121±4 (25)
	21	10±5 (24)	130±10 (22)	10±6 (20)	130±9 (20)	4±4 (20)	132±11 (20)
	22	16±5 (32)	131±7 (32)	16±3 (29)	131±7 (29)	8±4 (29)	132±6 (29)
	33	15±5 (24)	102±18 (24)	14±5 (22)	102±18 (22)	1±7 (22)	101±17 (22)
	34	17±4 (33)	133±6 (33)	17±4 (31)	133±6 (31)	4±3 (31)	135±6 (31)
	Ad(1)	14±3 (30)	122±7 (28)	14±3 (26)	123±6 (29)	4±3 (28)	125±7 (28)
	Ad(2)	19±7 (31)	126±10 (31)	20±6 (29)	127±7 (29)	1±5 (29)	119±12 (29)

Values are means ± s.d. (N =number of steps) of touch-down and lift-off angles as well as minimum (Min) and maximum (Max) angles during stance and swing phase.

For abbreviations, see Table 3.

bending and tilting could not be analysed, because of the 2D-projection of the X-ray. Therefore, only craniocaudal 'pelvic movements' were evaluated.

Position of the pelvis at touch-down was similar in adults of both species (Table 4). During stance phase, the pelvis moved caudally and was a bit more inclined at lift-off. Effective and maximal angular movements during stance and swing were very low in adults of both species (4° to 7° and 10° to 17° , respectively). During the development of the tree shrew, no change occurred in mean touch-down or lift-off position, or effective and maximal angular movements. Even from their first steps, juvenile pelvic angles were similar to those of adults. In the cui, however, the pelvis was more protracted during the locomotion of the youngest age stages. Mean pelvic angle at touch-down on the day of birth was only 130° , and it increased to 140° and 148° during development. Comparisons of effective angular movements during development showed that the pelvis was more inclined throughout the step cycle in the youngest animals. From P5, values varied individually, but were more or less similar to those of adults.

Femur

The femur was almost horizontal at touch-down in adult tree shrews and cui (Table 4). The femur retracted during stance phase, and reached its maximum excursion at the end of stance. The femur was clearly more caudally rotated in adult tree shrews than in adult cui. As shown by its higher maximum

excursion, the femur was held nearly vertical during lift-off in the adult cui (81° and 91°), whereas it was much more retracted in the tree shrew (125°). Protraction of the femur began shortly before lift-off and continued until the end of swing. The femur rotated through the horizontal in some steps of adults of both species. Mean minimum angle of swing was comparable between the adults of both species. Femur retraction began before touch-down and continued until the end of stance. Despite comparable cranial excursions, the effective and maximum angular movements of femur in adult tree shrews exceeded that of cui because of greater caudal excursions.

Mean femur angle at touch-down was not significantly correlated with age or body mass in either species. That is, touch-down position of the femur remained unchanged during postnatal development. Lift-off angle increased with increasing body mass in the tree shrew, however, the correlation was not significant. In the cui, mean lift-off angles increased with increasing age and body mass ($r=0.72$; $P\leq 0.05$). The smallest observed mean lift-off angle of 36° was found in the newborn cui and the femur angle at lift-off approached adult values after the first week of life. The femur was never retracted past the vertical in young cui below 50 g body mass. In young tree shrews, the femur always passed through a vertical position, but it was more retracted in the under nourished animal P39(2). Adult values were not reached by the time the tree shrews left the nest (Table 4). Effective

angular movements of the femur of juveniles were lower than those of adults, because juveniles had smaller angles at lift-off, but a similar touch-down position. Although the minimum femur angle during stance and touch-down angle were similar in adults of both species, the minimum angle at touch-down was smaller in the juveniles. This was due to passive cranial displacement of the femur under load at touch-down in the younger animals. No passive protraction at touch-down was observed after the age of P5 in cui and P25 in tree shrew.

Shank

The shank reached a minimum angle at the end of swing phase with mean values of 60° and 59° in adult tree shrews and 51° in adult cuis. Retraction of the shank started shortly before touch-down (Table 4). Shank retraction continued until the end of stance, reaching a more caudally rotated position in the adults cuis than the adult tree shrews. The shank passed the horizontal in both species. Minimum shank angle during stance phase was the same as mean lift-off angle in the cui, whereas in the tree shrew, the shank was rotated cranially until it reached a mean lift-off angle of -1° and -6°. That is, the shank was positioned nearly horizontally at lift-off in adult tree shrews and more inclined in cui. As the foot left the ground, the shank continued retracting until it reached its minimum angle during swing. The subsequent protraction continued until just before touch-down when the maximum angle during swing phase was reached.

Mean touch-down position of the shank was independent of age or body mass in both species. Touch-down angles were slightly higher than in older animals only in the youngest cuis. Mean lift-off angle was horizontal in young cuis and decreased significantly with age and body mass ($r=0.57$ and 0.53 , respectively; $P\leq 0.05$), while in tree shrews, shank angle increased significantly with increasing age and body mass, approaching a more horizontal position ($r=0.88$ and 0.87 , respectively; $P\leq 0.001$). By P39, shank values of the normal weight animal were similar to those of adults, while values of the underweight animal were comparable to younger individuals of the same body mass.

Foot

Tarsus and metatarsus were analysed together as one segment. Touch-down position was semi-digitigrade in adults of both species with a mean foot angle of 9° and 14° in tree shrews and 14° and 19° in cuis (Table 4). During stance, the foot was retracted until it reached its maximum caudal rotation at lift-off. Mean lift-off angles were comparable between the adults of both species. After lift-off, which included a quick retraction of the foot, protraction began, and continued until the end of swing phase. The foot was held horizontally in some step cycles of adults of both species during swing phase. Mean minimum angles ranged between 4° and -1° in adults of both species.

Whereas no change in touch-down position of the foot occurred during the development of the tree shrew, mean touch-down angle decreased with increasing age and body

mass in the cui ($r=0.58$ and 0.60 , respectively; $P\leq 0.05$). Retraction of the foot at lift-off increased with age in both species. Lift-off angle was positively correlated with age in the cui ($r=0.49$, $P\leq 0.05$) and more correlated with age than with body mass in the tree shrew ($r=0.82$, $P\leq 0.001$ and $r=0.78$, $P\leq 0.01$, respectively). Adult values were reached after the first week of life in the precocial young of the cui and by the time they left the nest in the altricial young of the tree shrew (P39). Effective angular movements of the foot were lower in juveniles than in adults of both species.

Hip joint

Mean touch-down angle of the hip joint was similar in adults of both species (tree shrew, 35° and 30°; cui, 33° and 45°). During stance, the hip joint extended and reached its maximum extension shortly before lift-off (tree shrew, 145° and 144°; cui, 112° and 116°). Maximum angle during stance and mean lift-off angle of adult tree shrews (141° and 142°) exceeded those of cuis (104° and 112°). Flexion of the hip joint began at the end of stance and continued into the following swing phase. Adults of both species had similar minimum hip joint angles during swing phase (22° to 30°). The hip joint in adults of both species was not flexed by loading at touch-down. Higher effective angular movement in adult tree shrews than in adult cuis was due to greater extension at the end of stance.

Whereas mean hip joint angle at touch-down decreased during development in the tree shrew with increasing body mass ($r=0.60$; $P\leq 0.05$), touch-down position was unchanged during development in the cui. Mean lift-off angles were significantly correlated with age in the tree shrew ($r=0.60$, $P\leq 0.05$) and with age and body mass in the cui ($r=0.86$ and 0.89 , respectively; $P\leq 0.001$). The hip joint was increasingly extended at lift-off during development. Even in the youngest tree shrews, mean lift-off angles exceeded those of adult cuis. By P39, the hip joint was only slightly more flexed than in adult tree shrews. With a mean lift-off angle of 112°, the hip joint of the underweight tree shrew P39(2) was more flexed than that of any other tree shrew in this study. After reaching 1 week old, values of precocial cui juveniles were comparable to those of adults. A quick passive flexion in the hip joint at touch-down due to loading was observed for the first three age stages of both species. Therefore, mean touch-down angles and minimum angles during stance were not the same in these individuals. Mostly due to the more flexed position of the hip at lift-off, the effective angular movement of younger individuals was lower than that of the adults in both species.

Knee joint

At touch-down, the knee joint was a little more extended in adult tree shrews (65° and 59°) than in adult cuis (49° and 55°). During stance, the knee was flexed to angles of 44° to 55° and extended until just before lift-off. The knee joint of adult tree shrews reached extension angles (126° and 121°) that were twice those of adult cuis (64° and 75°). Consequently, mean lift-off angles in adult cuis (56° and 59°) were much lower than

those of adult tree shrews (124° and 119°). Flexion of the hip joint during swing reached minimum angles of 42° and 33° in the adult tree shrews and 28° and 35° in the adult cuis.

Mean knee angle at touch-down was not correlated with age or body mass in the tree shrew. In contrast, mean touch-down angle decreased with increasing age and body mass in the cui ($r=0.55$ and 0.49 , respectively; $P\leq 0.05$). Mean knee angle at lift-off was significantly positively correlated with age and body mass in both species (tree shrew: $r=0.56$ and 0.68 , $P\leq 0.05$, respectively; cui: $r=0.61$ and 0.64 , $P\leq 0.01$, respectively). Mean lift-off angles of the youngest tree shrews exceeded those of all investigated stages of the cui. As in the hip joint, the underweight tree shrew juvenile P39(2) had the lowest value at lift-off of all the individuals studied (84°). Mainly due to significant changes in lift-off angle, effective and maximum angular excursions increased during ontogeny. Therefore, the knee joint was more extended at touch-down than at lift-off in younger cuis until P9, when this relation was reversed. In tree shrews, knee angles were always higher at lift-off than at touch-down.

Ankle joint

At touch down, the ankle joint was similarly flexed in the adults of both species (tree shrew, 58° and 62° , cui, 59° and 51°). During the first half of stance phase, the ankle joint underwent dorsal flexion and reached mean minimum angles which were similar in both species (47° to 50°). Extension of the ankle lasted until the end of stance phase and maximum extension during stance and mean lift-off angle were nearly the same in both species (tree shrew, 137° and 118° ; cui, 98° and 103°). Higher values in adult tree shrews were due to greater plantar flexion of the ankle joint at lift-off. Minimum angle during swing phase was reached after lift-off (34° to 43°) and was followed by a short extension. Flexion of the ankle joint started shortly before touch-down and continued into stance phase. Effective and maximum angular movements of the ankle joint were higher in adult tree shrews than in cuis because of greater plantar flexion.

During postnatal development of the cui, mean touch-down angle decreased with increasing age and body mass ($r=0.57$ and 0.56 , respectively; $P\leq 0.05$). Despite increasing dorsal flexion of the foot at touch-down during development, lift-off position remained unchanged. The opposite was true for the tree shrew. Although mean touch-down position of the ankle joint was not significant correlated with age or body mass, mean lift-off position increased with increasing age and body mass ($r=0.81$, $P\leq 0.001$ and $r=0.78$, $P\leq 0.01$, respectively). By P39 in the tree shrew and after the first week of life in the cui, ankle position had reached adult values.

Summary of developmental changes in kinematics

Beginning with their first steps, all individuals had the typical zigzag limb configuration of adults (Fig. 5). Furthermore, the general timing of segment and joint angle movements did not change during development. Limb position at touch-down was comparable to that of adults in the first steps

of both species. In tree shrews, only mean touch-down angle of the hip joint decreased with increasing body mass during postnatal development. In cuis, mean touch-down angles of the scapula, hand and foot, as well as knee and ankle joints, decreased with increasing age or body mass. No other segment or joint angles changed during development.

Developmental changes in limb performance were considerable at lift-off. Out of the 14 investigated segment and joint angles, 11 in the tree shrew and 10 in the cui changed during development. Caudal displacement of the scapula, lower arm, hand, femur and foot increased with increasing age or body mass in both species. In contrast, the position of the humerus and shank changed differently during development in the two species. Whereas both segments were held horizontally at the end of stance in adult tree shrews, they were clearly held above the horizontal in juveniles until they left the nest. In cuis, lift-off angles of humerus did not change during development. Retraction of the shank increased from a horizontal position at birth to adult values by P5. The shank was retracted more caudally in the cui than in the tree shrew. The underweight juvenile tree shrew had values for most segment and joint angles more similar to those of similar sized younger animals than to those of the tree shrew of the same age.

Contribution of segment movements to stance length

The contribution of each segment's movement to stance length depends on the height of pivot, and the angular excursion and length of the segment. Therefore, more proximal limb segments contribute more to forward displacement than more distal ones (Table 5). Independent of age or body mass, the scapula and femur contributed the highest percentage to stance length in both species. The scapula contributed 34–46% of stance length in tree shrews and 44–60% in cuis. Angular movement of the femur clearly contributed more to stance length in tree shrews than in cuis (Table 5). Contributions to stance length by the distal elements were independent of age and body mass and did not change during development in either species. The angular excursion of the hand contributed 5–17% of stride length in both species. In the hindlimb, the contribution of the phalanges to stance length was very low in most individuals and zero in others (-18% to -3%).

The contribution of the middle segments of the forelimb to stance length changed drastically during development. In both species, the contribution of the excursion of humerus to stance length decreased during development (tree shrew: from 44% at P14 to 18% in adults; cui: from 37% at P0 to 8% in adults). Whereas lower arm rotation did not contribute stride length in the youngest animals (tree shrew P14, 8%; cui P0, 1%), its contribution increased to one third of stance length by the end of the investigated developmental period. Despite these developmental changes in the forelimb, the contribution of foot rotation was one third of stance length irrespective of age or body mass in both species. Whereas shank movement contributed to stride length in young cuis,

it did not contribute in older animals [P0 18%, adult (2) -4%]. The shank did not contribute to stance length in any tree shrew (-7% to -18%).

Discussion

Invariable parameters

A recent comparison of adults of eight species has led to the

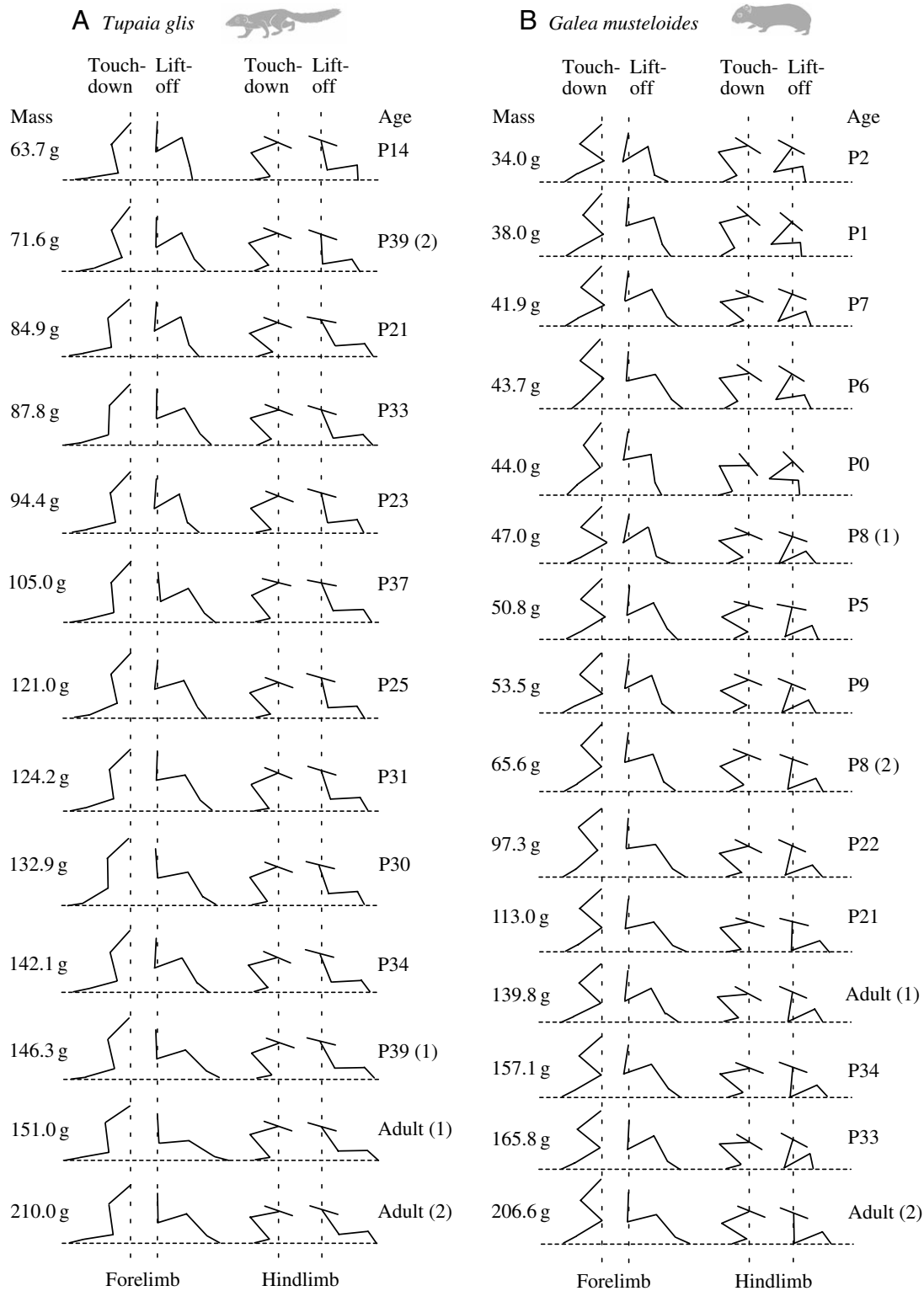


Fig. 5. Mean touch-down and lift-off positions of fore- and hindlimb of (A) *Tupaia glis* and (B) *Galea musteloides* sorted by body mass. Note the constant touch-down position of both fore- and hindlimb and the increasing retraction of limb segments at lift-off. Also the underweight tree shrew P39(2) is comparable in its kinematic parameters to younger individuals of the same body mass.

identification of basic principles of the locomotion of small to medium-sized therian mammals that are independent of systematic relationships and natural habitats (Fischer et al., 2002). In brief, the three-segmented limbs were held in zigzag configuration, and rotated by the dorsalmost pivot point (scapular pivot and hip joint during symmetrical gaits). The pivots of fore- and hindlimbs were at the same height above the ground and thus resulted in similar functional limb lengths. In the double-flexed limbs, two segments (scapula and lower arm or femur and foot) were oriented in the same direction and coordinated during retraction of the limb. In this study of locomotor ontogeny, these general movement patterns were observed in the altricial and precocial juveniles from their first steps. No major changes in overall limb performance were observed during postnatal ontogeny.

Segmental and joint movements of adults of different mammalian species began at the end of stance or swing phase shortly before touch-down or lift-off and lasted continuously into the next phase (Fischer, 1994; Schilling and Fischer, 1999; Fischer and Lehmann, 1998; Schmidt and Fischer, 2000;

Fischer et al., 2002). The onset of protraction and retraction was not coupled to the events of touch-down and lift-off. For instance, retraction of all limb segments started in the last third of swing phase during symmetrical gaits. At lift-off, the proximal limb segments (scapula and femur) were already in protraction (Fischer et al., 2002). From birth, the timing of segment and limb joint movements was similar to that in adults; no developmental changes in timing occurred. Leg retraction just prior to ground contact is a common principle in animal locomotion. The effect of leg retraction was employed with a conservative spring mass model (Seyfarth et al., 2003) but also with biomechanical models for quadrupedal locomotion (Herr et al., 2002) in order to test its effect on running stability. In all models, leg retraction could significantly improve stability and swing-phase limb dynamics played an important role in stabilisation of running animals (Herr et al., 2002; Seyfarth et al., 2003).

Touch-down position of almost all limb segments and joints was nearly constant during postnatal ontogeny. The point of touch-down of forelimbs was below the eye in all juveniles.

Table 5. Contribution of segment movements to stance length (%) for all individuals of both species

Age (days)	Body mass (g)	Forelimb				Hindlimb			
		sc	hu	la	ha	fe	sh	ft	ph
<i>Galea musteloides</i>									
0	44.0	56	37	1	7	62	18	26	-6
1	38.0	52	26	17	5	47	41	10	3
2	34.0	51	24	15	11	62	25	11	2
5	50.8	53	15	23	9	66	1	31	2
6	43.7	57	6	28	9	64	12	25	0
7	41.9	47	18	30	6	64	8	27	1
8(1)	47.0	44	26	15	16	70	10	18	2
8(2)	65.6	52	25	11	13	70	-1	30	1
9	53.5	49	24	17	9	63	3	34	0
21	113.0	53	6	33	8	80	-5	43	-18
22	97.3	60	13	20	8	61	1	36	3
33	165.8	56	10	22	11	81	0	16	3
34	157.1	52	14	28	6	68	-3	38	-4
Ad(1)	139.8	54	16	20	10	72	-3	27	3
Ad(2)	206.6	52	8	34	6	72	-4	31	2
<i>Tupaia glis</i>									
14	63.7	40	44	8	8	93	-13	27	-2
21	84.9	43	36	3	17	81	-18	37	1
23	94.4	40	43	2	16	77	-8	30	1
25	121.0	36	44	3	17	76	-16	37	3
30	132.9	46	31	6	17	84	-13	28	1
31	124.2	43	31	13	13	81	-13	32	0
33	87.8	38	39	7	16	86	-17	31	0
34	142.1	34	41	12	13	86	-15	28	1
37	105.0	41	36	11	12	82	-14	31	2
39(1)	146.3	39	29	21	11	77	-14	36	1
39(2)	71.6	46	39	-2	17	78	-7	29	0
Ad(1)	151.0	44	18	33	6	80	-16	31	4
Ad(2)	210.0	41	29	23	7	90	-17	28	-1

sc, scapula; hu, humerus; la, lower arm; ha, hand; fe, femur; sh, shank; ft, foot; ph, phalanges. For further abbreviations, see Table 1.

Examinations of adults of different therian species confirm the invariance of touch-down point and touch-down limb position (Fischer et al., 2002). Therefore, touch-down turns out to be the most standardized event during locomotion in both juveniles and adults. Touch-down is a crucial event during the step cycle because it is the moment that the body first comes in contact with the ground and it is the beginning of limb support. Flexion of the joints and foot placement are highly standardized at this crucial moment, which possibly enables the animal to react to unexpected ground conditions. The flexed limb can be further flexed or extended to adjust to unexpected obstacles. In both adults (Fischer et al., 2002) and juveniles (this study), modulations of stride duration and stride length took place primarily at lift-off, the less critical point in the stride cycle. The highly standardized touch-down position is therefore hypothesized as a 'kinematic goal' of limb movement, which has to be reached at the beginning of each stride cycle to ensure stability of the body and to prevent torsions of the body axis. The uniformity of touch-down positions has to be addressed in further studies in order to test this hypothesis.

Variable parameters

Major changes in limb position occurred at lift-off during locomotor ontogeny. In both species, mean lift-off angles of the scapula, lower arm, femur and foot increased during development. This resulted in higher extensions at most limb joints as the animals matured. From the moment that the phalanges passed below the elbow joint during stance, the flexors must prevent passive extension of the elbow caused by gravity; EMG-activity of the extensors (m. triceps brachii) is reduced in small mammals (Fischer, 1999; Scholle et al., 2001). By changing the activation of the flexors, the joints may be flexed or extended. In juveniles, the lower arm and femur are held nearly vertically at lift-off. Juveniles avoided large caudal limb excursions over the vertical position, possibly because of weaker flexor muscles. Extensors are more mature than flexors because they are used earlier in ontogeny to elevate the body (Fox, 1964). Higher tone in extensor muscles than flexors was described in various species independent of their life histories (Fox, 1963). Early development of the extensors may be connected to fact that the first steps of juveniles use the adult touch-down position.

Until age P5 in *Galea musteloides* and P25 in *Tupaia glis* [except for P39(2)] a slight protraction of the scapula and humerus was observed at touch-down. These movements could be passively evoked by gravity during limb loading. Perhaps the muscle force of younger animals is not strong enough to resist gravity, or the timing of muscle activity is immature. But as Carrier (1983) pointed out for *Lepus californicus*, some juveniles are able to produce relatively larger forces, per unit body mass, than adults, leading to higher accelerations in the juveniles. Therefore, immature muscle activity patterns in juveniles such as increased latencies between bursts, irregular activation patterns of muscles independent from the movement, co-activation of muscles, or the activity level of a

given muscle (Geisler et al., 1996; Gramsbergen et al., 1997, 1999) are more likely responsible for the protraction of both segments at ground contact.

Younger individuals of both species had higher scapular angles at touch-down than older animals, which resulted in a more vertical position and therefore lower forces required to maintain this position. Investigations of the dynamics of forelimbs in small mammals, especially *Galea musteloides*, showed that the resultant ground reaction force was oriented caudal to the shoulder joint (Witte et al., 2002). If it were assumed that the orientation of the ground reaction force is similar in juveniles and adults at touch-down (no data are available for small juvenile mammals), the ground reaction force would be nearly parallel to the scapular spine. The length of the lever arm from the scapular pivot to the ground reaction force is much shorter if the scapula is oriented more vertically than if it is horizontal. Therefore, the muscle force necessary to maintain the scapula's position during touch-down is less with the more vertical orientation of the scapula in juveniles than with the more inclined position in adults. The vertical orientation of the scapula at ground contact (initiation of load, body mass) may be due to the immaturity of the shoulder muscles.

Vilensky and Gankiewicz (1989) and Howland et al. (1995) studied developmental changes in the hindlimb movement of *Cercopithecus aethiops* and *Felis catus* f. *domestica* using videos. With increasing age, flexion at all limb joints decreased and the limbs became more erect. The greater extension of hindlimb joints of *Cercopithecus aethiops* and *Felis catus* f. *domestica* resulted in more erect limb posture than in the smaller species studied here. Extensive studies of the developmental changes in hindlimb kinematics during over ground locomotion in *Rattus norvegicus*, using external markers, were reported by Westerga and Gramsbergen (1990, 1993a,b). Mean lift-off angles at the knee and hip joints decreased during development. In contrast, extension of limbs increased during the development of *Tupaia glis* and *Galea musteloides*.

The limbs are mainly retracted during stance phase and protracted during swing phase (Fischer et al., 2002). While segment movements are exclusively monophasic, joint movements can be biphasic containing two flexions and two extensions per stride. Joint movements vary from species to species. *Cercopithecus aethiops* showed monophasic shoulder joint movements (Whitehead and Larson, 1994) while *Felis catus* f. *domestica* (English, 1978; Boczek-Funcke et al., 1996) and *Eulemur fulvus* (Schmidt and Fischer, 2000) exhibit biphasic joint behaviour during symmetrical gaits. In *Tupaia glis*, shoulder joint movements depended on gait (Schilling and Fischer, 1999). Biphasic movements were observed during symmetrical gaits but were reduced to monophasic movements at asymmetrical gaits. During postnatal development, the monophasic movement of the shoulder joint exhibited by younger *Tupaia glis* changed to the adult, biphasic pattern. No changes in joint movements occurred during the development of the precocial *Galea musteloides*.

A limb segment's relative contribution to stride length depends on its angular excursion, the height of its pivot, and its length (Fischer and Lehmann, 1998). Comparison of the contribution of segment movement to step length clearly showed that the proximal limb segments (scapula, femur) produced more than half of total stride length during symmetrical gaits in adults (Fischer et al., 2002). This was also true in the juveniles studied here. As a result of the increased rotation of the lower arm during development, the contribution of the lower arm increased to one third of stance length in both species. For the hindlimb, a significant change in the contributions of the segments during development only occurred in *Galea musteloides*. In younger cuis, the shank was positioned nearly horizontally and, in this orientation, it contributed its entire length to stride length. During development, the shank became more inclined ($<-20^\circ$ in adults) and contributed less to stride length.

Reproductive biology

Different patterns of postnatal development have evolved in eutherian mammals. Species range from the ancestral state of naked juveniles with closed eyes and ears, completely dependent upon maternal care (e.g. rats, mice or tree shrews), to the derived state of fully haired young, which feed themselves and are capable of locomotor activity at birth (e.g. horses, hares or cuis; Sánchez-Villagra and Sultan, 2002).

Contrary to all expectations, the same developmental changes in limb configuration and movement were found in both precocial and altricial species. Only the time necessary for these developmental changes to occur was different between the species. The adult kinematic pattern was reached after the first week in the precocial young of the cui and by the time they would leave the nest in the altricial juvenile tree shrews. During the evolution of precocial development, only processes independent of exercise or gravity could be shifted into the prenatal phase, such as the development of the overall distribution pattern of muscle fiber types in limb muscles (von Mering and Fischer, 1999; Schilling and Fischer, 2001; N. S., personal observation). The development of locomotor ability is dependent on use and gravity and must occur during postnatal growth. Therefore, the same developmental changes were observed in both species.

Individuals of comparable age but different body mass were included in the current study to test whether development is more dependent on chronological age or on body mass. Differences in body mass were especially evident in the tree shrew. In the majority of cases, developmental changes in kinematics were more closely linked to body mass than to age. In particular, the underweight juvenile tree shrew had kinematic parameters more similar to younger individuals of the same body mass than to individuals of its age group. Similar results were found in *Rattus norvegicus* and *Ovis aries* (Yamaguchi et al., 1993; Joubert, 1955) and this is consistent with the work of Portmann (1965), who pointed out that time is not an appropriate variable to choose when comparing developmental stages.

Conclusions

Developmental changes were unexpectedly similar in the two species studied here. Despite the advanced state of maturity at birth in the juvenile cuis, the same kinematic parameters changed during postnatal development as in the altricial juvenile tree shrews. The first steps of precocial juveniles were not the same as those of adults. Adult kinematic parameters were reached after 1 week of age in young cuis, and by the time they would leave the nest in juvenile tree shrews. A 1-week-old precocial cui is comparable in its developmental maturity to a weaned altricial tree shrew (P39–41). The postnatal time necessary to gain locomotor maturity in precocial young is one third of the time necessary for the ancestral altricial state of mammalian young. The development of locomotor ability depends on limb use and gravity and therefore must occur in the postnatal phase. During the evolution of precocial juveniles, this developmental period was clearly shortened.

Touch-down position of nearly all limb segments and joints was independent of age or body mass in juveniles (this study) and of gait and velocity in adults (Schilling and Fischer, 1999; Fischer et al., 2002; Witte et al., 2002), while lift-off position varied with speed and gait in adults, and with age or body mass during development. As the moment of first ground contact, touch-down position may be a kinematic goal that must be reached at the beginning of each step cycle. Therefore, no major developmental changes were found in the touch-down position. The earlier development of extensors in comparison to flexors allows the animal to use adult touch-down position in its first steps, while lift-off position changed as flexors matured during postnatal ontogeny. Development of most kinematic parameters depended more on mass than on chronological age, as demonstrated by the addition of underweight individuals of certain age classes.

I thank M. S. Fischer and D. R. Carrier for stimulating discussions and valuable comments on the manuscript. I thank all members of the work group at Jena, and especially M. Schmidt and K. E. Lilje for valuable discussions. D. Haarhaus and R. Hackert assisted with the cinevideography, and M. Roser helped with some figures. J. S. Markley thoroughly revised the manuscript. This study was funded by the German Research Foundation (DFG) (Innovation college 'Motion systems' projects A1 and B1, Fi 410/1-3).

References

- Altman, J. and Sudarshan, K. (1975). Postnatal development of locomotion in the laboratory rat. *Anim. Behav.* **23**, 896-920.
- Blumberg-Feldman, H. and Eilam, D. (1995). Postnatal development of synchronous stepping in the gerbil (*Meriones tristis*). *J. Exp. Biol.* **198**, 363-372.
- Boczek-Funcke, A., Kuhtz-Buschbeck, J. P. and Illert, M. (1996). Kinematic analysis of the cat shoulder girdle during treadmill locomotion: an X-ray study. *Eur. J. Neurosci.* **8**, 261-272.
- Bradley, N. S. and Smith, J. L. (1988a). Neuromuscular patterns of stereotypic hindlimb behaviors in the first two postnatal months. I. Stepping in normal kittens. *Dev. Brain Res.* **38**, 37-52.
- Bradley, N. S. and Smith, J. L. (1988b). Neuromuscular patterns of

- stereotypic hindlimb behaviors in the first two postnatal months: III. Scratching and the paw-shake response in kittens. *Dev. Brain Res.* **38**, 69-82.
- Carrier, D. R.** (1983). Postnatal ontogeny of the musculo-skeletal system in the Black-tailed jack rabbit (*Lepus californicus*). *J. Zool. London* **201**, 27-55.
- Dene, H., Goodman, M. and Prychodko, W.** (1978). An immunological examination of the systematics of Tupaiidae. *J. Mamm.* **59**, 697-706.
- Eilam, D.** (1997). Postnatal development of body architecture and gait in several rodent species. *J. Exp. Biol.* **200**, 1339-1350.
- Eilam, D. and Shefer, G.** (1997). The developmental order of bipedal locomotion in the Jerboa (*Jaculus orientalis*): Pivoting, creeping, quadrupedalism, and bipedalism. *Dev. Psychobiol.* **31**, 137-142.
- English, A. W.** (1978). Functional analysis of the shoulder girdle of cats during locomotion. *J. Morph.* **156**, 279-292.
- Fischer, M. S.** (1994). Crouched posture and high fulcrum, a principle in the locomotion of small mammals: The example of the rock hyrax (*Procapra capensis*) (Mammalia: Hyracoidea). *J. Hum. Evol.* **26**, 501-524.
- Fischer, M. S.** (1999). Kinematics, EMG, and inverse dynamics of the therian forelimb – a synthetic approach. *Zool. Anz.* **238**, 41-54.
- Fischer, M. S. and Lehmann, R.** (1998). Application of cineradiography for metric and kinematic study of in-phase gaits during locomotion of pika (*Ochotona rufescens*, Mammalia: Lagomorpha). *Zoology* **101**, 148-173.
- Fischer, M. S. and Witte, H. F.** (1998). The functional morphology of the three-segmented limb of mammals and its specialities in small and medium-sized mammals. *Proc. Eur. Mech. Coll. Euromech.* **375**, 10-17.
- Fischer, M. S., Schilling, N., Schmidt, M., Haarhaus, D. and Witte, H. F.** (2002). Basic limb kinematics of small therian mammals. *J. Exp. Biol.* **205**, 1315-1338.
- Fox, M. W.** (1963). The development and clinical significance of muscle tone and posture in the neonate dog. *Am. J. Vet. Res.* **24**, 1232-1238.
- Fox, M. W.** (1964). A phylogenetic analysis of behavioral neuro-ontogeny in precocial and non-precocial mammals. *Can. J. Comp. Med. Vet. Sci.* **28**, 197-202.
- Geisler, H. C., Westerga, J. and Gramsbergen, A.** (1993). Development of posture in the rat. *Acta Neurobiol. Exp.* **53**, 517-523.
- Geisler, H. C., Westerga, J. and Gramsbergen, A.** (1996). The function of the long back muscles during postural development in the rat. *Behav. Brain Res.* **80**, 211-215.
- Gramsbergen, A., Aa, M. v. d. and Geisler, H. C.** (1997). Aspects of postural development in the rat. *Equine Vet. J.* **23**, 66-70.
- Gramsbergen, A., Geisler, H. C., Taekema, H. and Eykern, v. L. A.** (1999). The activation of back muscles during locomotion in the developing rat. *Brain Res. Dev. Brain Res.* **112**, 217-228.
- Herr, H. M., Huan, G. T. and McMahon, T. A.** (2002). A model of scale effects in mammalian quadrupedal running. *J. Exp. Biol.* **205**, 959-967.
- Honacki, J. H., Kinman, K. E. and Koeppl, J. W.** (1982). *Mammal Species of the World – A Taxonomic and Geographic Reference*. Lawrence, Kansas, USA: Joint Venture of Allen Press.
- Howland, D. R., Bregman, B. S. and Goldberger, M. E.** (1995). The development of quadrupedal locomotion in the kitten. *Exp. Neurol.* **135**, 93-107.
- Jamon, M. and Clarac, F.** (1998). Early walking in the neonatal rat: A kinematic study. *Behav. Neurosci.* **112**, 1218-1228.
- Jenkins, F. A. J.** (1974). *Primate Locomotion*. New York, London: Academic Press.
- Jenkins, F. A. J. and Camazine, S. M.** (1977). Hip structure and locomotion in ambulatory and cursorial carnivores. *J. Zool. London* **181**, 351-370.
- Joubert, D. M.** (1955). Growth of muscle fibre in the foetal sheep. *Nature* **175**, 936-937.
- Nakano, Y.** (1996). Footfall patterns in the early development of the quadrupedal walking of Japanese macaques. *Folia Primatol.* **66**, 113-125.
- Peters, S. E.** (1983). Postnatal development of gait behavior and functional allometry in domestic cat (*Felis catus*). *J. Zool. London* **199**, 461-486.
- Portmann, A.** (1965). Über die Evolution der Tragzeit der Säugetiere. *Revue Suisse Zool.* **72**, 657-666.
- Sánchez-Villagra, M. R. and Sultan, F.** (2002). The cerebellum at birth in therian mammals, with special reference to rodents. *Brain Behav. Evol.* **59**, 101-113.
- Schilling, N. and Fischer, M. S.** (1999). Kinematic analysis of treadmill locomotion of tree shrews, *Tupaia glis* (Scandentia: Tupaiidae). *Int. J. Mamm. Biol.* **64**, 129-153.
- Schilling, N. and Fischer, M. S.** (2001). Postnatal development of muscles in small mammals. *J. Morph.* **248**, 281.
- Schilling, N., Hackert, R. and Fischer, M. S.** (1999). Vertebral column movements of small mammals during locomotion. *Zoology* **102**, 44.
- 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.
- Scholle, H. C., Schumann, N. P., Biedermann, F. H. W., Stegeman, D. F., Graßme, R., Roeleveld, K., Schilling, N. and Fischer, M. S.** (2001). Spatiotemporal surface EMG characteristics from rat triceps brachii muscle during treadmill locomotion indicate selective recruitment of functionally distinct muscle regions. *Exp. Brain Res.* **138**, 26-36.
- Seyfarth, A., Geyer, H. and Herr, H.** (2003). Swing-leg retraction: a simple control model for stable running. *J. Exp. Biol.* **206**, 2547-2555.
- Vilensky, J. A. and Gankiewicz, E.** (1989). Early development of locomotor behavior in vervet monkeys. *Am. J. Primatol.* **17**, 11-25.
- von Mering, F. and Fischer, M. S.** (1999). Fibre type regionalization of forelimb muscles in two mammalian species, *Galea musteloides* (Rodentia, Caviidae) and *Tupaia belangeri* (Scandentia, Tupaiidae), with comments on postnatal myogenesis. *Zoomorphology* **119**, 117-126.
- Westerga, J. and Gramsbergen, A.** (1990). The development of locomotion in the rat. *Dev. Brain Res.* **57**, 163-174.
- Westerga, J. and Gramsbergen, A.** (1993a). Changes in the electromyogram in two major hindlimb muscles during locomotor development in the rat. *Exp. Brain Res.* **92**, 479-488.
- Westerga, J. and Gramsbergen, A.** (1993b). Development of locomotion in the rat: The significance of the early moments. *Early Hum. Dev.* **34**, 89-100.
- Whitehead, P. F. and Larson, S. G.** (1994). Shoulder motion during quadrupedal walking in *Cercopithecus aethiops*: integration of cineradiographic and electromyographic data. *J. Hum. Evol.* **26**, 525-544.
- Witte, H. F., Biltzinger, J., Hackert, R., Schilling, N., Schmidt, M., Reich, C. and Fischer, M. S.** (2002). Torque patterns of the limbs of small therian mammals during locomotion on flat ground. *J. Exp. Biol.* **205**, 1339-1353.
- Yamaguchi, A., Horio, Y., Sakuma, S. and Katsuta, S.** (1993). The effect of nutrition on the size and proportion of muscle fibre types during growth. *J. Anat.* **182**, 29-36.