

Basic limb kinematics of small therian mammals

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Summary

A comparative study of quantitative kinematic data of fore- and hindlimb movements of eight different mammalian species leads to the recognition of basic principles in the locomotion of small therians. The description of kinematics comprises fore- and hindlimb movements as well as sagittal spine movements including displacement patterns of limb segments, their contribution to step length, and joint movements. The comparison of the contributions of different segments to step length clearly shows the proximal parts (scapula, femur) to produce more than half of the propulsive movement of the whole limb at symmetrical gaits. Basically, a three-segmented limb with zigzag configuration of segments is mainly displaced at the scapular pivot or hip joint, both of which have the same vertical distance to the ground. Two segments operate in matched motion during retraction of

the limb. While kinematic parameters of forelimbs are independent of speed and gait (with the scapula as the dominant element), fundamental changes occur in hindlimb kinematics with the change from symmetrical to in-phase gaits. Forward motion of the hindlimbs is now mainly due to sagittal lumbar spine movements contributing to half of the step length. Kinematics of small therian mammals are independent of their systematic position, their natural habitat, and also of specific anatomical dispositions (e.g. reduction of fingers, toes, or clavicle). In contrast, the possession of a tail influences ‘pelvic movements’.

Key words: in-phase gait, lumbar spine, locomotion, symmetrical gait, X-ray, small therian mammal.

Introduction

The evolution of mammalian limbs is marked by the transition from a two-segmented, sprawled tetrapod limb to a three-segmented limb (for a review, see Fischer, 1999) and from lateromedial, undulatory movements to dorsoventral movements of the body axis (Hildebrand, 1974). The addition of locomotory active segments is achieved in different ways for fore- and hindlimbs: the shoulder blade becomes moveable and is added as the proximal segment to the ‘old’ ancestral forelimb (Jenkins and Weijs, 1979), whereas on the hindlimb the existing distal element, the foot, is prolonged and becomes the third segment by the ‘new’ ankle joint. As a consequence serially homologous elements such as humerus and femur no longer functionally correspond to each other. The functional correspondence is now: shoulder blade to thigh, upper arm to lower limb, forearm to foot. These postural changes influence fundamentally the action of the limbs during locomotion.

Our first aim is to present quantitative kinematic data of fore- and hindlimbs’ movements for several, only distantly related, small therian mammals at different gaits. Based on this substantial amount of highly detailed work, a comparative study of limb configuration and kinematics was undertaken to look for basic kinematic similarities emerging together with the

new therian limb. The principles that emerge from these studies, together with the published work especially on cats will be also tested for their validity in midsize ungulates.

Another key innovation of therian locomotion is the regular use of in-phase gaits (gallop, half-bound, bound); crocodiles show gallop only exceptionally as juveniles (Zug, 1974). According to Hildebrand (1985), sagittal spine movements occur typically in fast carnivores, lagomorphs, and rodents. We present first data for other especially small therians. The consequences of these ‘new’ gaits on fore- and hindlimbs and especially lower spine kinematics have never been quantified using cineradiography. Based on the X-ray study of slow walking (i.e. exploratory walking) in the tree shrew *Tupaia glis*, a restricted bending region of flexion between Th11 and L1 has been described (Jenkins, 1974a). This observation will be tested in faster ‘in-phase’ gaits. In our study, we also included animals with and without tails, to test their influence on the kinematics of the sagittal back movements.

Cineradiography is the only tool that recognizes the exact kinematics of all proximal skeletal parts hidden under the skin and subcutaneous fat. Previous studies on quadrupedal therian mammals quantitatively analysed either (1) single joints such

as the shoulder joint in rats (*Rattus norvegicus*; Jenkins, 1974b), hip joint and back movements in the skunk (*Mephitis mephitis*; Van de Graaff et al., 1982), trunk movements in the shrew-like opossum (*Monodelphis domestica*; Pridmore, 1992), elbow and wrist joint in the potto (*Perodicticus potto*; Jouffroy et al., 1983), ankle joint in kangaroo rats (*Dipodomys spectabilis*; Biewener and Blickhan, 1988), single limbs at specific gaits (e.g. hindlimb in cats *Felis catus* f. domestica; Kuhtz-Buschbeck, 1994), or (2) qualitatively single steps only at one or more gaits (e.g. *Tupaia*; Jenkins, 1974a; jirds *Meriones shawi*; Gasc, 1993). Most data are available for the cat, which has long been used as a model organism (Engberg and Lundberg, 1969; Goslow et al., 1973; Miller and Van der Meché, 1975; Jenkins and Camazine, 1977; Sontag et al., 1978; English, 1978a,b, 1980; Halbertsma, 1983; Hoy and Zernicke, 1985; Caliebe et al., 1991; Kuhtz-Buschbeck et al., 1994; Boczek-Funcke et al., 1996, 1998, 1999). From outside of our group the only cineradiographic study on fore- and hindlimb kinematics at different gaits was published by Rocha Barbosa et al. (1996) on the domestic guinea pig *Cavia porcellus*.

Scapular displacement during quadrupedal locomotion has been measured in *Felis* (Miller and Van der Meché, 1975; English, 1978a; Sontag et al., 1978; Boczek-Funcke et al., 1996), *Rattus* (Jenkins, 1974b), *Cavia* (Rocha Barbosa et al., 1996), Virginia opossum, *Didelphis marsupialis* (Jenkins and Weijs, 1979) and vervet monkeys *Cercopithecus aethiops* (Roberts, 1974; Whitehead and Larson, 1994). The studies named describe a clear pro- and retraction of the shoulder blade during locomotion, but the impact of this displacement on step length and the overall kinematics of the forelimb has never been determined.

We have collected kinematic data on eight different small therian mammals using cineradiography. Data of two phylogenetically distant metatherians (*Dasyuroides byrnei*, *Monodelphis domestica*) and six eutherians belonging to five different orders (Primates: *Microcebus murinus*; Rodentia: *Galea musteloides*, *Rattus norvegicus*; Lagomorpha: *Ochotona rufescens*; Hyracoidea: *Procavia capensis*; Scandentia: *Tupaia glis*) are now available to elaborate upon the kinematic principles of small mammal locomotion. In addition, data based on analyses of two artiodactyls, *Tragulid javanicus* and the domestic goat *Capra hircus* (Lilje and Fischer, 2001), a very small rodent (*Acomys cahirinus*), as well as another

primate (*Saguinus oedipus*; Schmidt and Voges, 2001) are included in this paper (e.g. in illustrating touch-down and lift-off positions). Single kinematic studies including detailed information about metric parameters, footfall patterns and gait-specific kinematics, as well as intralimb timing are already published on *Procavia capensis* (Fischer, 1994, 1998), *Ochotona rufescens* (Fischer and Lehmann, 1998), *Tupaia glis* (Schilling and Fischer, 1999), and *Eulemur fulvus* (Schmidt and Fischer, 2000). These published data are drawn together here by further calculations, for example, on the contribution of limb segments to step length.

Materials and methods

Animals

Limb kinematics were studied by cineradiography in adult individuals of eight small therian species which belong to different higher-order taxonomic groups of mammals. The kinematic analyses are based on more than 80,000 digitised X-ray frames. Table 1 gives an overview of the species under investigation by denoting number of individuals, body mass and body length. For sake of simplicity, we named the species by their generic names only. All experiments were registered by the Committee for Animal Protection of the State of Thuringia, Germany.

Individuals were positively conditioned to move on a horizontal motor-driven treadmill within a Plexiglas enclosure (length 100 cm, width and height were adapted to the requirements of each species) except for the arboreal quadrupedal *Microcebus*, which walked on a rope-mill, an arboreal analogue of a treadmill. Treadmill speed was not fixed, but the operator attempted to keep the running animal in front of the X-ray screen for as long as possible. Thus, the operator adjusted the speed to obtain certain preferred speeds of the animals. Comparisons of treadmill locomotion and unrestrained locomotion have shown that the basic schemes of kinematics are the same in both situations (Fischer, 1999).

Cineradiography

The X-ray equipment consisted of an automatic Philips® unit (Type 9807 501800 01) with one X-ray source image-amplifier chain. Pulsed X-ray shots were applied

Table 1. Number, size characteristics of the eight species under study

	Number of individuals		Body mass (g)	Snouth-vent length (mm)
	Males	Females		
<i>Monodelphis domestica</i> (Metatheria)	2		92	82
<i>Dasyuroides byrnei</i> (Metatheria)	2		145	145
<i>Galea musteloides</i> (Rodentia)	1	1	300	216
<i>Rattus norvegicus</i> (Rodentia)	2	1	350	205
<i>Ochotona rufescens</i> (Lagomorpha)	2		250	191
<i>Procavia capensis</i> (Hyracoidea)	2		1200	280
<i>Tupaia glis</i> (Scandentia)	1	1	180	189
<i>Microcebus murinus</i> (Primates)	1		100	130

(approximately 50 kV, 200 mA). The X-ray images on the image intensifier were recorded either on 35 mm film using an Arritechno R35-150 camera or with a high-speed CCD camera (Mikromak Camsys®) operating at 150 frames s^{-1} . The animals were filmed in a lateral projection with a maximum exposure time of 10 s. As some of the animals were larger than the area of interest covered by the image-amplifier (20.5 cm \times 15.0 cm), fore- and hindlimbs were recorded separately. An orthogonal wire grid, perpendicular to the projection plane, provided reference points for correction of geometrical distortions and metrical calculations.

Processing of X-ray images

X-ray films were copied onto video tapes and A/D-converted using a video processing board (Screen Machine® I, Fast® Multimedia AG, Munich, Germany), and further analysed by application of the software 'Unimark 3.6' (by R. Voss). This software makes it possible to digitise interactively previously defined landmarks with a cursor function; it also corrects distortions automatically and calculate angles and distances. The positions of digitised landmarks and angles calculated in the parasagittal plane are illustrated in Fig. 1. Angles calculated are the projections of angles onto the sagittal plane representing their contribution to movements in the plane of forward motion.

The errors generated by digitisation of skeletal landmarks and their influence on the angles calculated were tested by repetitive digitisation (five times) of one sequence (25 frames) for each species. The digitisation error depends on the size of the animal and the image contrast of skeletal elements. It ranges from 0.5° to 2.0° for segment angles (see below) and is roughly 1.0–3.0° for joint angles, because the errors of two adjacent segment angles combine in joints following the Gaussian rules of error propagation.

Analysis of angular movements and their contribution to step length

Limb joint angles were defined anatomically and measured

at the flexor side of each joint. Segment angles were calculated *versus* the horizontal plane. We shall use the term protraction (= cranial rotation) for the cranial displacement of the distal end of each segment. Retraction (= caudal rotation) describes its caudal displacement. Maximum amplitudes of joint excursion during stance and swing phases were calculated from the initial moments of segment and limb-joint movements. Effective angular displacements (EAD) were defined as differences of angles at touch-down and lift-off. The ratio EAD *versus* maximum joint amplitudes gives the coefficient of stance phase (CSP). A ratio higher than 0.5 indicates a joint's action resulting in a forward propulsive movement.

Fischer and Lehmann (1998) proposed an 'overlay method' to calculate the relative contribution of angular movements to step length. While the CSP indicates the non-propulsive vertical work of joints, only the overlay method enables calculation of the relative contribution of segment movements to horizontal forward motion, because it considers the displacements of pivots of the limb segments during stance phase.

Summarising the 'overlay method' in short, the calculations are based on mean values of typical gait sequences, of which stance and swing phase duration are scaled to equivalent relative durations using the method of linear interpolation. A polynomial fit of sixth order is used to interpolate data. For calculation, angular values are defined in the vertical plane to be positive if the distal end of the segment is in front of the proximal end. The horizontal distance (l_p) between tip of toe and the pivot of the whole limb is determined for every single limb configuration during stance phase, using the lengths of segments and their angular excursions against the vertical plane. By overlaying the proximal segment onto the next configuration, without changing angles in the more distal joints, the difference between the horizontal excursion at instant i (l_{pi}) and at instant $i+1$ (l_{pi+1}) is the step length caused by the rotation of each particular segment. For each segment the absolute contribution to step length is given by the summation of all

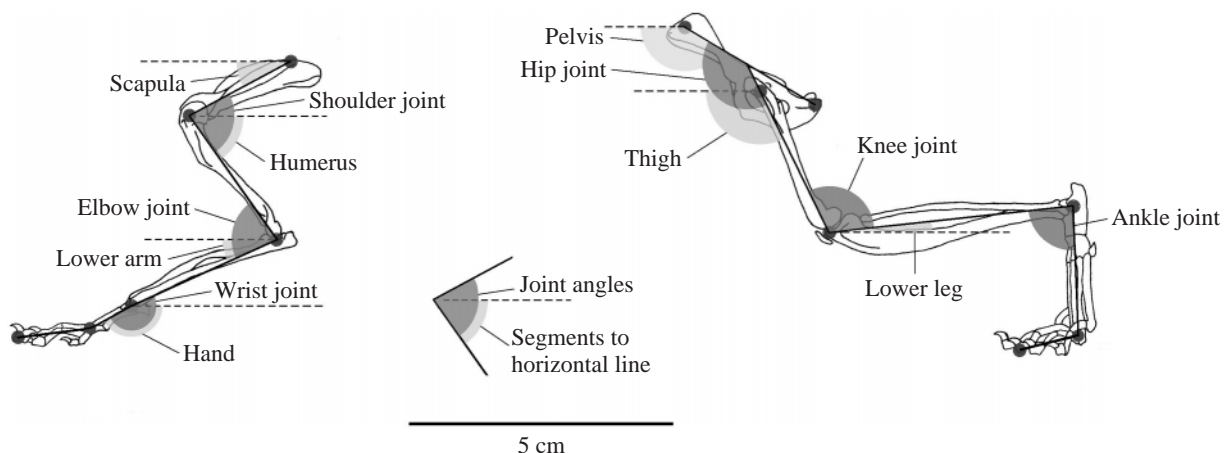


Fig. 1. Positions of captured skeletal landmarks and calculated angles of segments and joints projected onto the parasagittal plane.

Table 2. Kinematic parameters of forelimb segments and limb joint angles at (A) symmetrical and (B) in-phase gaits

	Touch down angle (degrees)			Lift-off angle (degrees)			Amplitude stance (degrees)			Contribution to step length (%)	Coefficient of stance	
	Mean	Range	N	Mean	Range	N	Mean	Range	N		Mean	N
(A) Symmetrical gaits												
Scapula												
<i>Monodelphis domestica</i>	37	29–42	18	90	75–106	17	59	50–72	16	53		
<i>Dasyuroides byrnei</i>	41	30–58	23	79	71–92	22	44	28–63	22	58		
<i>Galea musteloides</i>	39	32–48	27	96	85–104	29	60	51–69	27	73		
<i>Rattus norvegicus</i>	41	32–51	27	95	79–103	31	60	44–68	27	57		
<i>Procavia capensis</i>	51	39–66	44	101	83–120	44	53	22–80	44	63		
<i>Tupaia glis</i>	38	26–49	31	92	81–103	31	59	40–69	28	43		
<i>Microcebus murinus</i>	41	27–59	76	87	73–104	92	48	36–64	76	46		
Humerus												
<i>Monodelphis domestica</i>	62	39–76	18	–20	–29–14	17	84	69–96	16	25		
<i>Dasyuroides byrnei</i>	36	16–68	23	–21	–44–9	22	59	37–91	22	15		
<i>Galea musteloides</i>	62	38–73	27	–7	–14–0	28	71	59–82	27	11		
<i>Rattus norvegicus</i>	58	51–70	27	–18	–28–4	31	78	63–94	27	16		
<i>Procavia capensis</i>	65	25–97	47	–2	–16–16	47	83	48–113	15	18		
<i>Tupaia glis</i>	85	65–102	31	–12	–24–2	31	105	88–134	28	17		
<i>Microcebus murinus</i>	78	52–103	76	–5	–26–9	92	87	64–105	76	27		
Lower arm												
<i>Monodelphis domestica</i>	24	14–35	18	120	88–135	17	96	80–116	16	16		
<i>Dasyuroides byrnei</i>	36	24–46	23	107	84–133	22	72	53–109	22	22		
<i>Galea musteloides</i>	30	25–35	26	122	112–131	27	94	87–105	26	15		
<i>Rattus norvegicus</i>	24	18–33	27	120	106–130	29	100	84–110	27	18		
<i>Procavia capensis</i>	28	10–47	47	117	93–138	47	100	68–122	15	18		
<i>Tupaia glis</i>	8	1–15	31	138	101–156	31	133	99–152	28	32		
<i>Microcebus murinus</i>	11	4–39	72	112	95–128	84	102	82–121	72	20		
Hand												
<i>Monodelphis domestica</i>	10	3–24	18	104	64–154	17	103	59–154	16	6		
<i>Dasyuroides byrnei</i>	12	0–22	23	86	41–125	22	80	37–115	22	5		
<i>Galea musteloides</i>	33	25–46	26	119	96–155	27	95	70–122	26	1		
<i>Rattus norvegicus</i>	16	5–26	27	143	107–178	29	132	93–162	27	9		
<i>Procavia capensis</i>	40	18–67	45	133	103–153	45	100	77–130	15	1		
<i>Tupaia glis</i>	13	4–22	31	157	109–193	31	153	97–192	28	8		
<i>Microcebus murinus</i>	2	–13–16	59	75	23–128	84	78	34–136	58	7		
Shoulder joint												
<i>Monodelphis domestica</i>	99	77–113	18	71	58–88	17	47	30–62	16		0.62	16
<i>Dasyuroides byrnei</i>	75	51–101	23	59	37–73	22	29	9–51	22		0.56	22
<i>Galea musteloides</i>	101	91–110	27	89	79–99	28	23	16–32	27		0.50	27
<i>Rattus norvegicus</i>	99	89–110	27	77	57–89	31	38	25–52	27		0.56	27
<i>Procavia capensis</i>	115	88–138	44	100	72–121	44	30	11–53	44		0.53	44
<i>Tupaia glis</i>	123	105–141	31	80	58–98	31	60	40–89	28		0.70	28
<i>Microcebus murinus</i>	120	93–141	76	82	64–98	92	49	26–75	75		0.86	75
Elbow joint												
<i>Monodelphis domestica</i>	86	62–102	18	100	66–114	17	41	25–55	16		0.35	16
<i>Dasyuroides byrnei</i>	71	44–102	23	86	57–120	22	37	14–65	22		0.49	22
<i>Galea musteloides</i>	93	79–101	26	116	103–130	27	42	35–53	26		0.55	26
<i>Rattus norvegicus</i>	82	69–98	27	101	84–118	29	44	26–55	27		0.46	27
<i>Procavia capensis</i>	92	57–120	44	116	83–143	44	45	14–71	44		0.55	44
<i>Tupaia glis</i>	90	76–115	31	124	78–150	31	70	30–93	28		0.47	28
<i>Microcebus murinus</i>	85	61–105	74	101	76–117	89	40	24–61	74		0.38	72
Wrist joint												
<i>Monodelphis domestica</i>	194	178–203	18	196	114–234	17	71	43–133	16		0.25	16
<i>Dasyuroides byrnei</i>	205	192–224	23	201	166–251	22	53	33–82	22		0.45	22
<i>Galea musteloides</i>	186	181–199	26	193	181–222	27	37	26–49	26		0.25	26
<i>Rattus norvegicus</i>	188	177–200	27	157	115–197	29	92	55–127	27		0.34	27
<i>Procavia capensis</i>	168	150–183	39	162	139–191	39	25	8–49	39		0.59	39
<i>Tupaia glis</i>	176	163–186	31	154	100–191	31	86	43–142	28		0.25	28
<i>Microcebus murinus</i>	187	172–201	63	215	168–248	89	76	46–109	63		0.42	57

Table 2. Continued

	Touch down angle (degrees)			Lift-off angle (degrees)			Amplitude stance (degrees)			Contribution to step length (%)	Coefficient of stance	
	Mean	Range	N	Mean	Range	N	Mean	Range	N		Mean	N
(B) In-phase gaits												
Scapula												
<i>Monodelphis domestica</i>	42	29–61	43	84	72–93	44	45	25–60	40	52		
<i>Dasyuroides byrnei</i>	45	33–64	18	80	67–90	18	37	25–48	18	55		
<i>Galea musteloides</i>	47	39–57	38	92	86–100	39	47	38–55	38	59		
<i>Ochotona rufescens</i>	46	20–70	318	80	51–100	318	37	7–65	318	66		
<i>Procavia capensis</i>	54	45–68	28	101	94–110	28	48	32–64	28	80		
<i>Tupaia glis</i>	46	36–61	17	85	66–95	12	47	37–67	12	47		
Humerus												
<i>Monodelphis domestica</i>	52	8–80	43	–23	–35–13	44	78	28–104	40	26		
<i>Dasyuroides byrnei</i>	46	22–64	18	–11	–25–5	18	59	36–85	18	25		
<i>Galea musteloides</i>	52	42–62	38	–3	–13–4	39	60	49–76	38	10		
<i>Ochotona rufescens</i>	61	20–89	316	–1	–24–23	316	62	20–101	316	23		
<i>Procavia capensis</i>	59	30–87	31	9	–3–16	31	36	26–59	8	–9		
<i>Tupaia glis</i>	86	63–106	17	–13	–31–2	12	100	72–128	12	45		
Lower arm												
<i>Monodelphis domestica</i>	25	8–41	43	112	94–128	44	88	73–107	40	19		
<i>Dasyuroides byrnei</i>	45	32–59	18	111	102–123	18	66	48–77	18	13		
<i>Galea musteloides</i>	39	24–52	38	128	119–135	39	89	67–101	38	27		
<i>Ochotona rufescens</i>	33	12–61	316	96	57–123	316	64	23–96	316	8		
<i>Procavia capensis</i>	46	26–62	31	118	97–127	31	68	56–82	8	29		
<i>Tupaia glis</i>	18	6–28	17	105	88–124	12	87	80–101	12	3		
Hand												
<i>Monodelphis domestica</i>	4	–7–16	39	65	2–120	44	64	8–118	36	3		
<i>Dasyuroides byrnei</i>	36	20–62	18	130	97–152	18	97	66–130	18	7		
<i>Galea musteloides</i>	29	12–47	38	134	107–159	39	109	81–141	38	4		
<i>Ochotona rufescens</i>	14	–2–56	316	86	21–157	316	75	17–154	316	3		
<i>Procavia capensis</i>	52	32–85	31	132	114–143	31	70	58–94	8	0		
<i>Tupaia glis</i>	17	10–28	12	136	114–156	12	126	100–147	9	5		
Shoulder joint												
<i>Monodelphis domestica</i>	94	66–126	43	61	47–75	44	40	7–70	40		0.82	40
<i>Dasyuroides byrnei</i>	91	61–113	18	69	46–91	18	29	10–48	18		0.74	18
<i>Galea musteloides</i>	99	91–110	38	89	80–95	39	26	15–37	38		0.96	38
<i>Ochotona rufescens</i>	107	80–140	318	80	50–105	318	30	1–63	318		0.91	318
<i>Procavia capensis</i>	114	90–136	28	110	101–117	28	23	10–37	28		0.5	28
<i>Tupaia glis</i>	132	107–153	17	72	62–82	12	60	31–91	12		0.98	12
Elbow joint												
<i>Monodelphis domestica</i>	77	43–103	43	89	62–108	44	43	28–58	40		0.39	40
<i>Dasyuroides byrnei</i>	91	69–108	18	101	86–116	18	28	6–42	18		0.45	18
<i>Galea musteloides</i>	91	82–98	38	125	108–137	39	54	32–73	38		0.62	38
<i>Ochotona rufescens</i>	94	68–120	318	96	60–120	318	20	0–45	318		0.51	318
<i>Procavia capensis</i>	106	81–130	28	127	104–136	28	38	18–55	28		0.53	28
<i>Tupaia glis</i>	104	82–124	17	91	65–107	12	41	24–62	12		0.46	12
Wrist joint												
<i>Monodelphis domestica</i>	202	181–217	43	227	164–297	44	62	42–91	36		0.56	40
<i>Dasyuroides byrnei</i>	188	163–202	18	165	139–205	18	43	19–80	18		0.65	18
<i>Galea musteloides</i>	190	171–210	38	174	152–200	39	51	28–71	38		0.36	38
<i>Ochotona rufescens</i>	200	159–235	318	190	102–255	318	42	2–127	318		0.49	318
<i>Procavia capensis</i>	175	152–185	28	165	147–177	28	24	8–37	28		0.49	28
<i>Tupaia glis</i>	183	167–198	13	149	115–174	12	72	51–112	9		0.46	9

single-frame calculations in stance phase. Finally, the contribution of the remaining segments to forward motion is calculated in the same way, except for the subtraction of the angular movement achieved by the sagittal rotation of the

more proximal segment(s). The relative contribution of segment displacement to step length depends on the pivot's height, the effective angular displacement (EAD) and the length of the segment.

Results

Fore- and hindlimb kinematics were studied by cineradiography in eight small therian species. At least 15, but up to 300, step cycles (period between two successive touch-downs of one limb) were analysed within broad ranges of running speeds (*Galea*, 0.3–1.3 m s⁻¹, *Dasyuroides*, 0.3–1.0 m s⁻¹, *Microcebus*, 0.3–1.7 m s⁻¹, *Monodelphis*, 0.4–2.4 m s⁻¹, *Procavia*, 0.2–2.1 m s⁻¹, *Ochotona*, 0.2–1.6 m s⁻¹, *Rattus*, 0.4–0.8 m s⁻¹, *Tupaia*, 0.5–1.6 m s⁻¹). Each species preferred different gaits within even the same speed ranges; e.g. *Rattus* and *Microcebus* only used ‘walk’ but pikas only used ‘halfbound’ and ‘gallop’. Because most animals changed both frequently and suddenly between walk and trot, or gallop and halfbound, we pooled walk and trot data as symmetrical gaits, as well as gallop and halfbound as in-phase gaits.

Kinematic data comprise segment and joint angles at touch-down and lift-off, maximum amplitude of the stance phase, contribution of segment displacement to step length and the coefficient of stance for limb joints at symmetrical gaits (Tables 2A, 3A) and in-phase gaits (Tables 2B, 3B,C). Differences between trailing and leading limbs (first and second touch-down) were observed on the hindlimbs only at gallop and half bound and therefore, these limbs are presented separately.

The following description of the kinematics of small mammalian locomotion is divided into three main parts: forelimb, spine movement, and hindlimb. The sections on limb kinematics start with the displacement pattern of the limb segments and their contribution to step length, followed by the description of joint movements.

Forelimb

Kinematics of forelimb segments

Segment displacements consist mainly of retraction during the stance phase and protraction during the swing phase. In all species, retraction of all segments starts before touch-down at 90–95% of the previous step cycle duration at symmetrical gaits and at 80% of the previous step duration at in-phase gaits (Fig. 2A,B). Scapular protraction begins at 85–90% of stance duration at symmetrical gaits but its timing is more variable at in-phase gaits. The beginning of humeral protraction varies around lift-off at all gaits, whereas forearm protraction is timed to coincide with lift-off at symmetrical gaits or with 10% of swing duration at in-phase gaits. Protraction of the hands begins late in the first third of swing. Fig. 2A,B illustrates the high uniformity of segment displacements (except of the hand) in all species.

Forelimb protraction and retraction are executed mainly by scapular displacement, as the most proximal segment. Retraction of the scapula begins from the most flexed position at 35–40° in the late swing phase. Mean touch-down angles of the scapula range within 37–51° at symmetrical gaits and 42–54° at in-phase gaits. In those species in which symmetrical as well as in-phase gaits could be analysed, an increased scapular touch-down angle was observed at in-phase

gaits. A continuous retraction of the scapula leads to a nearly vertical orientation at the end of stance. Rotary movement then stops and in acylavicate species such as *Procavia*, a translatory gliding along the thoracic wall follows (for details, see Fischer, 1994). Mean scapular lift-off angles are between 79° and 101° at symmetrical gaits and are in approximately the same range at in-phase gaits (Table 2A,B). Mean amplitudes of scapular retraction are maximally 10% higher than the differences of angles at touch-down and lift-off. The greatest amplitude of scapular retraction was measured in the rodents (60° for both species) and in *Monodelphis* and *Tupaia*, each with 59°.

In all species, humeral displacement is as uniform as scapular movement (Fig. 2A,B). Mean touch-down angles for five species are in a small range of less than 10° (58–65° at symmetrical gaits, 52–61° at in-phase gaits). *Tupaia* and *Microcebus* have a more protracted upper arm at touch-down with mean angles of 85° and 78°, respectively (Fig. 4). In contrast, *Dasyuroides* has the most retracted humerus at touch-down, being only 36° at symmetrical gaits and 46° at in-phase gaits. This species also shows the lowest overall amplitude of humeral displacement at 59° and *Tupaia* the highest amplitude of humeral retraction at 105° (Table 2A). Retraction of the humerus starts before touch-down and is already completed at midstance. Afterwards, the humerus is positioned more or less horizontally and held in this position until the first quarter of the swing phase (*Procavia* -2°, *Galea* -7° and *Microcebus* -5° at symmetrical gaits; *Procavia* 9°, *Galea* -3° and *Ochotona* -1° at in-phase gaits). *Monodelphis*, *Dasyuroides* and *Rattus* elevate the humerus more above the horizontal line (mean angle between -18° and -21° at symmetrical gaits).

The forearm is in matched motion with the scapula (i.e. both segments are displaced nearly parallel to each other), especially during the stance phase (Fig. 2B). Mean touch-down angle is highly uniform at symmetrical gaits and ranges between 24° and 36° with the exception of *Tupaia* (8°) and *Microcebus* (11°) in which – by stronger protraction of the humerus and not by elbow flexion (see below) – the forearm is placed almost parallel to the ground. At in-phase gaits, the mean touch-down angle is more variable within our sample of species and lies between 18° in *Tupaia* and 46° in *Procavia*. Retraction of the forearm continues until the end of stance phase and ends at lift-off at symmetrical gaits, or at 10% of the swing phase at in-phase gaits. Lift-off angle varies slightly between species (107–122°) at symmetrical gaits. Only *Tupaia* deviates from this position with a more retracted forearm (138°) and thus has the greatest overall amplitude of forearm movement (133°). The mean lift-off angle has a broader range at in-phase gaits. The lowest values were observed in *Ochotona* (96°) and *Tupaia* (105°), whereas *Galea* has the highest lift-off angle at 128°.

The hand is placed in a semidigitigrad position; a digitigrad position was frequently observed only in *Procavia*. In *Microcebus*, walking on a rope-mill, the hand grasps around the circumference of the rope. Here, hand and wrist joint angles also were projected onto the sagittal plane. Hand displacements

Table 3. Kinematic parameters of hindlimb segments and limb joint angles at (A) symmetrical and (B,C) in-phase gaits. Trailing and leading limbs are presented separately in (B) and (C) respectively

	Touch down angle (degrees)			Lift-off angle (degrees)			Amplitude stance (degrees)			Contribution to step length (%)	Coefficient of stance	
	Mean	Range	N	Mean	Range	N	Mean	Range	N		Mean	N
(A) Symmetrical gaits												
Pelvis												
<i>Monodelphis domestica</i>	33	21–42	18	31	21–39	16	12	5–25	16	–3		
<i>Dasyuroides byrnei</i>	28	5–45	21	23	9–31	19	17	8–32	19	7		
<i>Galea musteloides</i>	22	14–29	47	19	14–27	48	10	6–18	47	3		
<i>Rattus norvegicus</i>	36	32–43	25	35	28–43	27	7	4–11	23	–3		
<i>Ochotona rufescens</i>	37	28–47	30	35	30–42	30	10	6–19	29	4		
<i>Procavia capensis</i>	51	36–68	21	47	30–60	21	14	5–31	21	7		
<i>Tupaia glis</i>	19	9–30	33	16	6–27	33	13	6–23	30	2		
<i>Microcebus murinus</i>	42	25–60	77	37	26–49	86	14	7–28	76	10		
Thigh												
<i>Monodelphis domestica</i>	8	0–20	18	92	59–109	16	84	70–101	16	93		
<i>Dasyuroides byrnei</i>	3	–15–26	21	51	14–89	19	51	24–85	19	59		
<i>Galea musteloides</i>	24	10–37	75	100	83–116	76	76	59–101	74	84		
<i>Rattus norvegicus</i>	7	–4–14	25	66	58–76	27	60	45–84	23	69		
<i>Ochotona rufescens</i>	14	–2–22	30	61	49–70	30	51	36–69	29	67		
<i>Procavia capensis</i>	–7	–18–4	22	60	30–95	22	71	55–83	11	52		
<i>Tupaia glis</i>	16	2–29	33	125	102–143	33	110	91–126	29	82		
<i>Microcebus murinus</i>	1	–12–27	76	76	53–96	85	78	40–98	75	93		
Lower leg												
<i>Monodelphis domestica</i>	84	69–96	18	14	3–21	16	71	60–81	16	–1		
<i>Dasyuroides byrnei</i>	59	37–76	21	–2	–9–9	19	61	46–85	19	15		
<i>Galea musteloides</i>	41	29–53	75	–14	–26–7	76	55	43–64	74	–9		
<i>Rattus norvegicus</i>	73	63–84	25	–3	–17–5	27	77	69–84	23	18		
<i>Ochotona rufescens</i>	65	56–72	30	–1	–6–7	30	66	51–76	29	19		
<i>Procavia capensis</i>	82	66–101	22	–4	–14–6	22	93	82–103	11	26		
<i>Tupaia glis</i>	49	33–60	33	–1	–20–11	33	59	48–76	29	–21		
<i>Microcebus murinus</i>	87	63–98	76	16	–5–33	76	71	56–98	75	–7		
Foot												
<i>Monodelphis domestica</i>	7	–1–14	18	105	80–139	14	97	74–131	13	11		
<i>Dasyuroides byrnei</i>	13	–3–33	21	92	67–118	19	81	46–118	19	19		
<i>Galea musteloides</i>	12	5–23	73	117	99–130	74	105	85–121	72	22		
<i>Rattus norvegicus</i>	8	–4–15	24	102	77–118	26	95	79–110	23	16		
<i>Ochotona rufescens</i>	11	2–17	30	91	71–103	30	80	59–98	29	10		
<i>Procavia capensis</i>	18	7–35	22	137	103–165	22	124	103–144	11	15		
<i>Tupaia glis</i>	9	–1–17	32	138	128–151	31	129	114–150	29	37		
<i>Microcebus murinus</i>	16	1–47	77	109	86–132	77	95	87–124	67	4		
Hip joint												
<i>Monodelphis domestica</i>	41	32–48	18	123	98–141	16	86	70–103	16		0.96	16
<i>Dasyuroides byrnei</i>	31	21–51	21	73	40–98	19	46	18–80	19		0.9	19
<i>Galea musteloides</i>	40	34–47	47	115	103–126	48	75	59–88	47		0.99	47
<i>Rattus norvegicus</i>	43	28–54	25	102	93–109	27	60	45–78	23		0.96	23
<i>Ochotona rufescens</i>	51	44–61	30	96	86–106	30	49	29–60	29		0.99	7
<i>Procavia capensis</i>	45	29–56	21	107	86–139	21	70	50–100	21		0.89	21
<i>Tupaia glis</i>	35	27–46	33	141	116–156	33	110	92–123	30		0.96	30
<i>Microcebus murinus</i>	43	27–54	76	113	85–135	85	75	56–92	75		0.9	75
Knee joint												
<i>Monodelphis domestica</i>	92	78–104	18	106	74–127	16	44	28–58	16		0.42	16
<i>Dasyuroides byrnei</i>	62	47–84	21	49	24–86	19	25	9–49	19		0.67	19
<i>Galea musteloides</i>	65	56–74	75	86	67–109	76	28	11–52	74		0.73	74
<i>Rattus norvegicus</i>	79	61–93	25	63	53–74	27	24	13–34	23		0.73	23
<i>Ochotona rufescens</i>	79	66–87	30	61	53–71	30	21	11–34	29		0.32	7
<i>Procavia capensis</i>	76	57–96	21	58	24–96	21	45	30–63	21		0.52	21
<i>Tupaia glis</i>	65	52–79	33	124	82–151	33	72	44–100	30		0.8	30
<i>Microcebus murinus</i>	88	68–109	76	92	60–129	85	30	15–54	75		0.4	75

Table 3. *Continued*

	Touch down angle (degrees)			Lift-off angle (degrees)			Amplitude stance (degrees)			Contribution to step length (%)	Coefficient of stance	
	Mean	Range	<i>N</i>	Mean	Range	<i>N</i>	Mean	Range	<i>N</i>		Mean	<i>N</i>
(A) Symmetrical gaits												
Ankle joint												
<i>Monodelphis domestica</i>	91	74–104	18	118	83–151	13	66	32–102	13		0.42	13
<i>Dasyuroides byrnei</i>	72	51–93	21	91	66–124	19	34	14–68	19		0.57	19
<i>Galea musteloides</i>	53	46–60	73	103	84–120	74	53	32–72	72		0.94	72
<i>Rattus norvegicus</i>	81	70–88	24	99	75–121	26	36	22–48	23		0.48	23
<i>Ochotona rufescens</i>	76	71–83	30	90	75–106	30	30	17–39	29		0.57	7
<i>Procavia capensis</i>	101	84–115	21	133	102–167	21	60	24–98	21		0.53	21
<i>Tupaia glis</i>	58	47–70	32	137	108–151	31	88	60–107	29		0.9	29
<i>Microcebus murinus</i>	103	84–126	77	125	98–165	77	36	20–74	67		0.7	67
(B) In-phase gaits, trailing limb												
Pelvis												
<i>Monodelphis domestica</i>	46	36–55	42	3	–7–11	34	44	30–55	32	52		
<i>Dasyuroides byrnei</i>	53	45–59	11	13	6–22	10	40	29–51	10	52		
<i>Galea musteloides</i>	56	45–66	16	13	6–23	17	44	23–67	16	50		
<i>Ochotona rufescens</i>	73	46–85	107	49	32–78	107	27	3–45	107	53		
<i>Procavia capensis</i>	78	58–93	51	37	27–65	51	49	23–64	50	49		
<i>Tupaia glis</i>	45	27–60	14	11	4–25	14	35	18–52	14	45		
Thigh												
<i>Monodelphis domestica</i>	0	–26–31	42	98	69–122	34	98	61–133	32	47		
<i>Dasyuroides byrnei</i>	–6	–16–11	11	63	53–72	11	70	50–85	11	29		
<i>Galea musteloides</i>	–1	–18–8	16	86	67–105	17	88	66–123	16	36		
<i>Ochotona rufescens</i>	1	–13–14	107	47	12–83	107	50	15–87	107	8		
<i>Procavia capensis</i>	–9	–31–1	50	56	10–82	50	86	77–97	10	16		
<i>Tupaia glis</i>	5	–22–22	14	101	60–120	14	97	52–119	14	46		
Lower leg												
<i>Monodelphis domestica</i>	85	64–98	42	21	1–41	34	67	31–95	32	–10		
<i>Dasyuroides byrnei</i>	81	65–94	11	7	1–15	11	74	57–91	11	5		
<i>Galea musteloides</i>	71	55–95	16	–19	–25–10	17	90	75–112	16	6		
<i>Ochotona rufescens</i>	82	54–102	107	18	1–36	107	65	37–92	107	35		
<i>Procavia capensis</i>	100	81–113	50	3	–13–40	50	107	100–115	10	25		
<i>Tupaia glis</i>	56	45–72	14	–11	–18–1	14	70	54–94	14	–7		
Foot												
<i>Monodelphis domestica</i>	7	–9–30	42	98	63–135	34	94	60–128	32	11		
<i>Dasyuroides byrnei</i>	9	–2–27	11	109	103–114	7	97	76–112	7	14		
<i>Galea musteloides</i>	5	–1–13	16	110	93–128	17	105	91–129	16	8		
<i>Ochotona rufescens</i>	8	–3–29	107	78	17–125	107	73	14–121	107	4		
<i>Procavia capensis</i>	16	0–48	48	121	54–147	50	128	121–138	10	10		
<i>Tupaia glis</i>	12	4–19	14	107	65–120	11	95	52–112	11	16		
Hip joint												
<i>Monodelphis domestica</i>	46	23–67	42	101	79–128	34	56	33–82	32		0.95	32
<i>Dasyuroides byrnei</i>	47	37–63	11	77	68–84	9	33	21–41	9		0.88	9
<i>Galea musteloides</i>	55	45–64	16	99	90–111	17	50	39–71	16		0.9	16
<i>Ochotona rufescens</i>	74	49–92	107	95	68–120	107	26	5–60	107		0.78	107
<i>Procavia capensis</i>	67	45–94	50	93	51–114	50	38	20–69	49		0.7	49
<i>Tupaia glis</i>	49	38–56	14	112	85–127	14	64	35–78	14		0.98	14
Knee joint												
<i>Monodelphis domestica</i>	85	62–111	42	119	76–149	34	54	34–87	32		0.6	32
<i>Dasyuroides byrnei</i>	75	66–88	11	70	60–80	11	32	21–50	11		0.28	11
<i>Galea musteloides</i>	69	62–79	16	67	48–93	17	27	11–51	16		0.34	16
<i>Ochotona rufescens</i>	83	61–104	107	64	40–109	107	34	6–55	107		0.57	107
<i>Procavia capensis</i>	89	42–111	51	59	19–95	51	65	42–98	50		0.46	50
<i>Tupaia glis</i>	61	48–73	14	91	60–109	14	45	15–60	14		0.69	14
Ankle joint												
<i>Monodelphis domestica</i>	91	67–116	42	119	84–163	34	74	39–133	32		0.37	32
<i>Dasyuroides byrnei</i>	90	78–106	11	117	112–120	7	40	28–48	7		0.67	7

Table 3. Continued

	Touch down angle (degrees)			Lift-off angle (degrees)			Amplitude stance (degrees)			Contribution to step length (%)	Coefficient of stance	
	Mean	Range	<i>N</i>	Mean	Range	<i>N</i>	Mean	Range	<i>N</i>		Mean	<i>N</i>
(B) In-phase gaits, trailing limb												
<i>Galea musteloides</i>	76	64–94	16	91	68–114	17	42	25–67	16		0.36	16
<i>Ochotona rufescens</i>	90	57–130	107	97	55–134	107	35	12–70	107		0.44	107
<i>Procavia capensis</i>	115	88–152	49	125	92–150	51	63	33–87	48		0.27	48
<i>Tupaia glis</i>	69	59–78	14	94	64–110	12	40	12–58	12		0.67	12
(C) In-phase gaits, leading limb												
Pelvis												
<i>Monodelphis domestica</i>	46	36–55	42	3	–7–11	34	44	30–55	32	53		
<i>Dasyuroides byrnei</i>	52	45–58	11	12	4–21	10	40	29–53	10	51		
<i>Galea musteloides</i>	50	34–72	16	9	3–17	16	41	18–64	16	38		
<i>Ochotona rufescens</i>	73	45–92	104	43	30–78	104	31	0–51	104	65		
<i>Procavia capensis</i>	80	59–92	18	40	29–65	18	46	23–62	17	48		
<i>Tupaia glis</i>	38	19–56	14	2	–9–9	12	39	28–58	13	41		
Thigh												
<i>Monodelphis domestica</i>	0	–26–31	42	98	69–122	34	98	61–133	32	44		
<i>Dasyuroides byrnei</i>	–5	–14–9	11	70	44–111	11	75	39–125	11	28		
<i>Galea musteloides</i>	–5	–21–11	16	98	88–107	16	103	83–125	16	50		
<i>Ochotona rufescens</i>	–9	–27–27	104	52	25–76	104	61	23–100	104	10		
<i>Procavia capensis</i>	–14	–29–1	12	67	10–95	12	103	70–132	9	27		
<i>Tupaia glis</i>	0	–21–18	14	109	83–124	13	109	74–127	13	53		
Lower leg												
<i>Monodelphis domestica</i>	85	64–98	42	21	1–41	34	67	31–95	32	–8		
<i>Dasyuroides byrnei</i>	80	68–96	11	12	0–39	11	71	57–87	11	7		
<i>Galea musteloides</i>	71	60–87	16	–14	–27–6	16	86	64–105	16	2		
<i>Ochotona rufescens</i>	82	49–98	104	22	4–46	104	60	19–89	104	19		
<i>Procavia capensis</i>	98	71–109	13	6	–14–14	13	107	96–116	9	16		
<i>Tupaia glis</i>	61	34–78	14	–4	–20–10	13	71	49–87	13	–12		
Foot												
<i>Monodelphis domestica</i>	7	–9–30	42	98	63–135	34	94	60–128	32	11		
<i>Dasyuroides byrnei</i>	7	–1–17	11	103	81–114	7	94	81–106	7	14		
<i>Galea musteloides</i>	4	1–7	16	118	107–132	16	115	95–131	16	11		
<i>Ochotona rufescens</i>	5	–7–29	104	81	9–118	104	77	23–114	104	6		
<i>Procavia capensis</i>	19	5–50	12	126	97–142	13	122	105–150	9	9		
<i>Tupaia glis</i>	10	2–20	14	114	82–141	12	104	74–131	12	18		
Hip joint												
<i>Monodelphis domestica</i>	46	23–67	42	101	79–128	34	56	33–82	32		0.95	32
<i>Dasyuroides byrnei</i>	47	39–59	11	80	60–115	10	36	11–72	10		0.91	10
<i>Galea musteloides</i>	44	26–63	16	106	97–116	16	68	43–84	16		0.92	16
<i>Ochotona rufescens</i>	64	44–78	104	94	67–124	104	33	6–73	104		0.89	104
<i>Procavia capensis</i>	60	40–80	40	109	71–141	38	61	24–95	37		0.74	37
<i>Tupaia glis</i>	38	32–48	14	110	87–123	12	72	46–88	12		0.99	12
Knee joint												
<i>Monodelphis domestica</i>	85	62–111	42	119	76–149	34	54	34–87	32		0.6	32
<i>Dasyuroides byrnei</i>	75	67–86	11	74	60–88	10	31	18–48	10		0.41	10
<i>Galea musteloides</i>	66	50–84	16	84	62–97	16	36	24–52	16		0.50	16
<i>Ochotona rufescens</i>	73	46–94	104	74	53–108	104	22	5–58	104		0.56	104
<i>Procavia capensis</i>	75	42–100	39	79	19–104	39	61	40–87	38		0.3	38
<i>Tupaia glis</i>	75	36–126	13	91	58–129	13	57	24–79	13		0.76	13
Ankle joint												
<i>Monodelphis domestica</i>	91	67–116	42	119	84–163	34	74	39–133	32		0.37	32
<i>Dasyuroides byrnei</i>	87	76–98	11	113	97–123	7	40	23–49	7		0.67	7
<i>Galea musteloides</i>	75	62–90	16	104	80–125	16	54	32–74	16		0.55	16
<i>Ochotona rufescens</i>	87	68–115	104	104	60–137	104	35	4–70	104		0.54	104
<i>Procavia capensis</i>	110	76–147	39	134	77–161	39	70	51–99	38		0.37	38
<i>Tupaia glis</i>	71	53–86	14	110	80–144	12	54	28–86	12		0.7	12

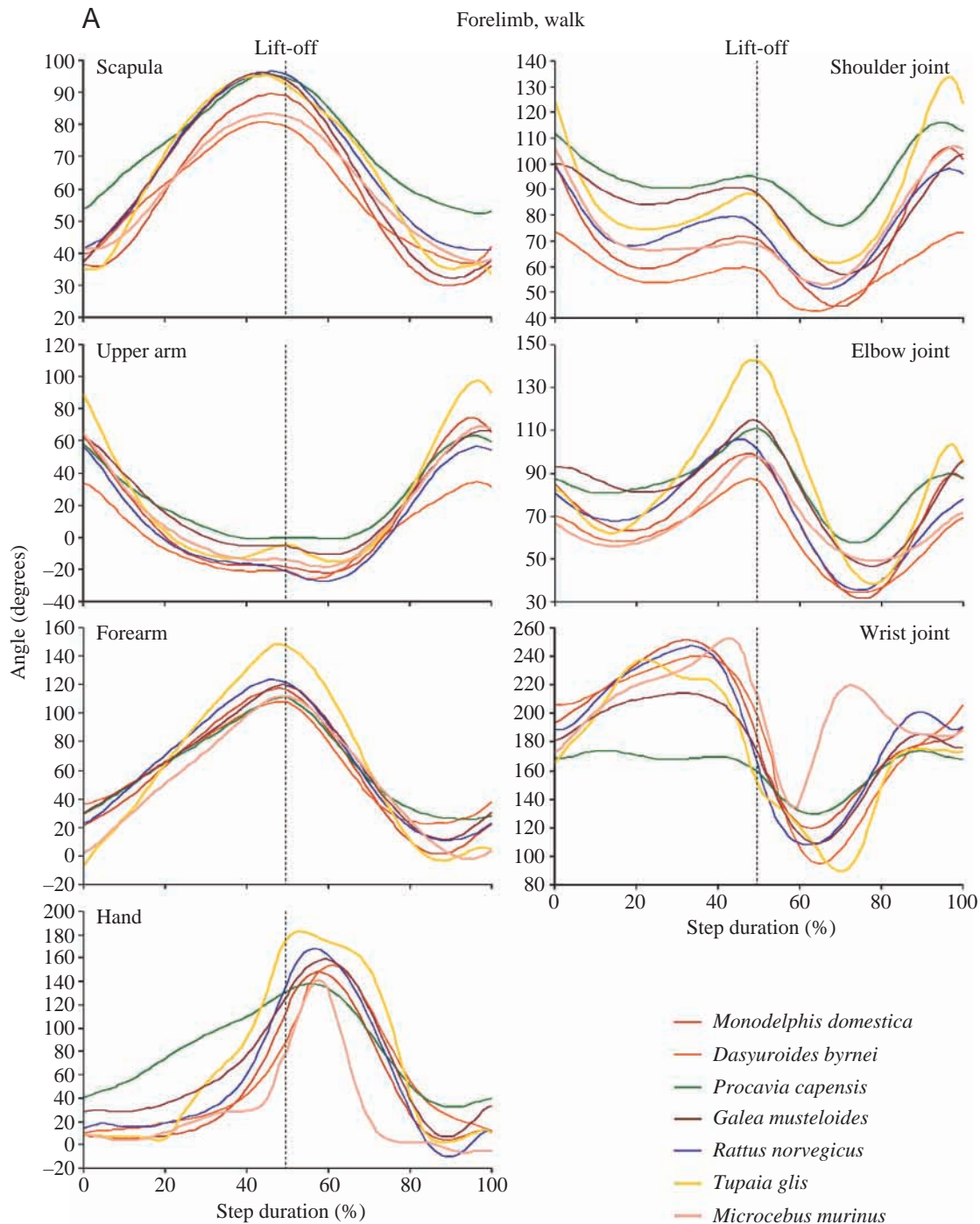
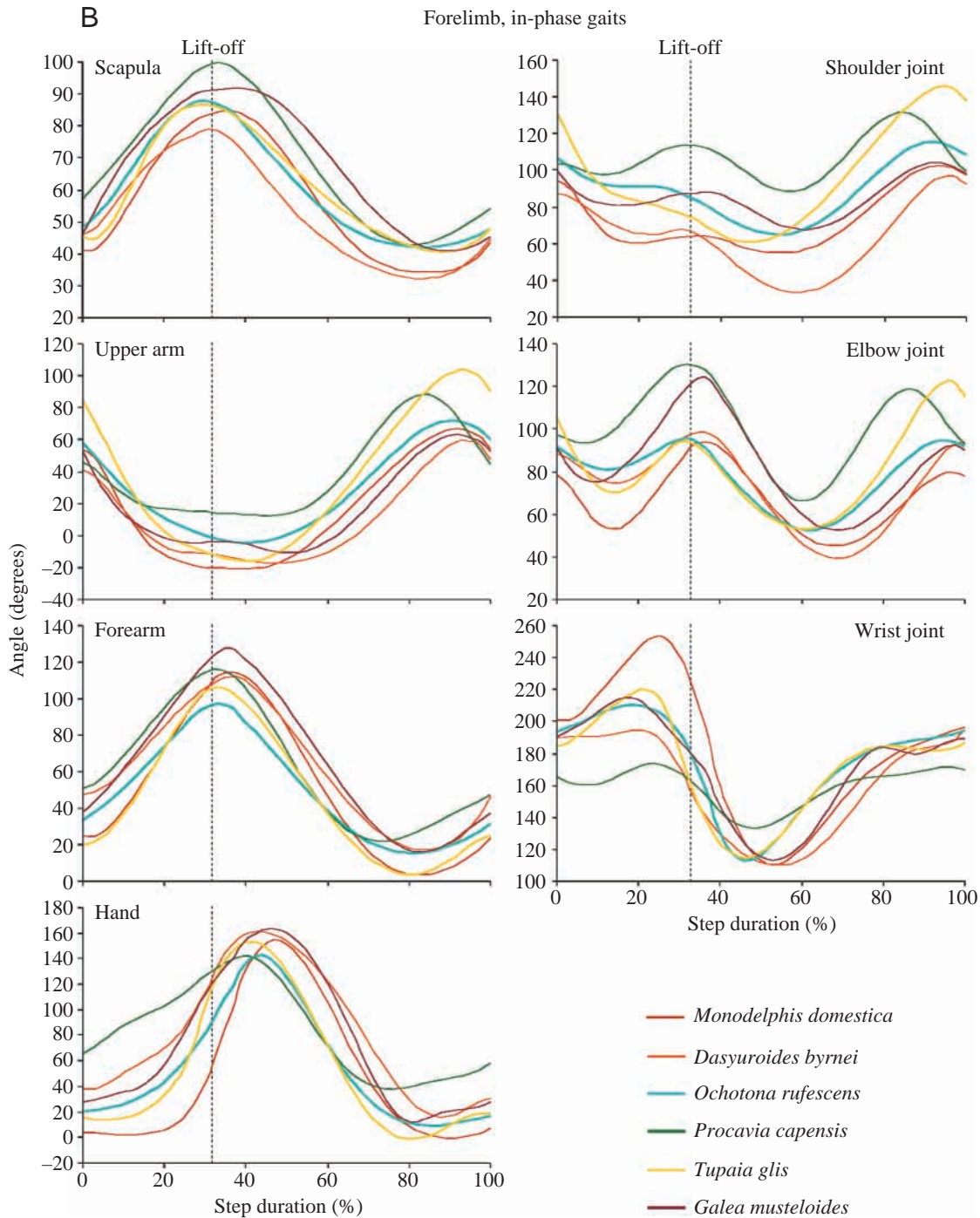


Fig. 2. Mean values of forelimb segment angular excursions of typical sequences at symmetrical (A) and in-phase (B) gaits. Stance and swing phases are scaled to the same duration using the method of linear interpolation. Based on this method the data for each limb segment are smoothed but their characteristics are preserved. Note the uniformity of time schemes especially of segment displacements despite differences for example in shoulder joint angular excursions.

are highly variable between all species as compared to the relative uniformity of displacements of the more proximal segments. Mean touch-down angles vary within broad ranges ($2\text{--}40^\circ$ at symmetrical gaits, $4\text{--}52^\circ$ at in-phase gaits). The highest angle value was measured in *Procavia* (Table 2A,B), in which the hand is displaced in a line with the forearm and

synchronised with it at the start of retraction and protraction (Fig. 2A,B). Hand retraction starts in the second half of the stance phase and ends in the first third of the swing phase in all species except *Procavia*. Mean lift-off angles are between 78° (*Microcebus*) and 157° (*Tupaia*) at symmetrical gaits, but at in-phase gaits *Tupaia* (136°), are closer to the values



observed in most other species (e.g. *Galea* 134°, *Dasyuroides* 130°, *Procavia* 132°). *Monodelphis* shows a relatively lower angle at these gaits (65°).

Contribution of forelimb segment movements to step length

The dissociation of segment and joint movements becomes obvious when the displacement of humerus, forearm and hand are compared with the effective angular movements in shoulder, elbow and wrist joints. Distal segments have a low degree of proper motion in the proximal adjacent joint and are

driven passively by the action of the more proximal segments. For example, the proper motion of the humerus in the shoulder joint of *Microcebus* during the stance phase accounts for only 48% of its amplitude. More than 50% of its humeral displacement results from scapular retraction alone and only 25% of its forearm displacement is actually achieved in the elbow joint.

Calculation of the contribution of segment movements to step length using the 'overlay method' (Fischer and Lehmann, 1998) indicates the predominance of scapular retraction in

forelimb movement. Scapular retraction accounts for more than 50% and up to 80% for step length in most species but for less than 50% in *Tupaia* and *Microcebus* (Table 2A,B). The high value in *Procavia* (80%) results from both the high scapular pivot and the amplitude at in-phase gaits. In contrast, the relative position of the scapular pivot in *Dasyuroides* is even higher than in *Procavia* (Fig. 4) but the amplitude of scapular retraction is low and, therefore, the overall contribution of the scapula is lower in *Dasyuroides* than in *Procavia*.

The relatively lower scapular contribution in both *Tupaia* and *Microcebus* is due to an overall increase in step length, caused in the first instance by a stronger protraction of the humerus and additionally by an extensive retraction of the forearm in *Tupaia*. Except for these two species, the contribution of humeral displacement to step length is always less than half of the scapular amount. The forearm contributes positively to step length only in the second half of the stance phase when its pivot (the elbow) raises. The forearm's contribution can exceed the value of the upper arm in species in which the forearm is retracted extensively; e.g. *Tupaia* at symmetrical gaits or *Galea* at in-phase gaits. The hand contributes to step length only in the last third of the stance phase when the wrist joint is lifted from the ground; in most species it contributes approximately 5% and never more than 10% to step length.

Kinematics of forelimb joints

In almost all species, the shoulder, elbow and wrist joints display biphasic angular movements during one step cycle for both symmetrical gaits and in-phase gaits (except for the wrist in *Procavia* and the shoulder in *Tupaia*; Fig. 2A,B). Phase relationships between different joints indicate that extensions in the shoulder, elbow and wrist joints are not synchronised. Flexion of all joints starts before touch-down, causing retraction of the segments. Flexion in the elbow joint reaches its maximum at 10–20% of step duration (20–40% of stance duration) (Fig. 2A,B), when the hand passes underneath the shoulder joint. Shoulder extension starts at midstance. The maximal dorsiflexion of the hand is reached at 65–70% of stance duration. The second flexion of the shoulder joint coincides with the beginning of scapula protraction at the end of the stance phase. The elbow flexion initiates protraction of the forearms while maximum plantarflexion of the wrist joint occurs only in the first half of swing phase. The shoulder joint is the first joint to extend during the swing phase; elbow extension then follows at 50% of the swing duration or later. An earlier extension of the elbow joint would counteract the forward movement of the limb. This sequence of forelimb joint movements during one step cycle is observed regularly in all species and at all gaits. Differences occur only in the degree of flexions and extensions, not in the intralimb coordination associated with the onset of movements.

In contrast to the amplitude of segment displacement, the amplitude of angular excursions in limb joints can be twice as high as the difference between the angles at touch-down and

lift-off (effective angular displacement, EAD), especially in the elbow and wrist joint (Tables 2A,B). The coefficient of stance phase (CSP), calculated as the ratio of EAD and the amplitude of joint excursion, indicates the degree of horizontal versus vertical action of joints. A CSP value of less than 0.5 indicates mainly vertically stretching and bending of the limbs and not to body protraction.

The shoulder joint has a relative high CSP in all species. It ranges between 0.50 and 0.86 at symmetrical gaits and increases for most of the species at in-phase gaits (except for *Procavia*). Mean shoulder joint angles at touch-down range at symmetrical gaits from 75° in *Dasyuroides* to 123° in *Tupaia*, and are between 91° (*Dasyuroides*) and 132° (*Tupaia*) at in-phase gaits (Table 2B). The mean lift-off angles are always smaller than touch-down angles and consequently, the resulting net joint movement of the shoulder joint is a flexion (except in *Procavia* at in-phase gaits). The variability of the lift-off angle is similar to that of the touch-down angle. In the first third of the stance phase, humeral retraction is faster than scapular caudal displacement, resulting in a flexion of the shoulder joint which ends at approximately 50% of the stance duration. The flexion is rather weak in *Procavia*, *Galea*, *Dasyuroides* and *Microcebus*. Flexion diminishes at in-phase gaits, an effect which is pronounced in *Monodelphis*. Shoulder joint movement in *Tupaia* is exceptionally monophasic at in-phase gaits, where the joint is continuously flexed during the whole of the stance phase and even until 26% of swing duration (Fig. 2B). The lowest overall amplitude of shoulder movement was found at symmetrical gaits in *Galea* (23°) and at in-phase gaits in *Procavia* (23°), the highest in *Tupaia* (60°).

In almost all species, the amplitudes of elbow joint excursions during the stance phase occur within a small range (37–45°) at symmetrical gaits (Table 2A). Only the amplitude of the elbow joint of *Tupaia* (70°) deviates from these values, as a consequence of extensive retraction of the forearm at the end of the stance phase. At in-phase gaits, the amplitudes of elbow joint movements vary over a broader range, between 20° in *Ochotona* and 54° in *Galea*. *Ochotona* has both a reduced flexion at midstance and a reduced re-extension at the end of the stance phase (Fig. 2B). Compared to the shoulder joint, the net joint movement of the elbow joint is an extension in almost all of the animals we sampled at all gaits (except for *Tupaia* at in-phase gaits). The mean touch-down angle of the elbow joint is usually smaller than the lift-off angle and ranges from 71° in *Dasyuroides* to 93° in *Galea* at symmetrical gaits. At in-phase gaits, the lowest mean touch-down angle was measured in *Monodelphis*. In the other species, the mean angles increase to as much as 106° in *Procavia*. Compared to the shoulder and wrist joint, the mean touch-down angle of the elbow joint is more constant in all species and at all gaits. However, the range of the mean lift-off angle is higher (86–124° at symmetrical gaits, 89–127° at in-phase gaits). *Tupaia* shows the highest mean lift-off angles at symmetrical gaits (124°), whereas the highest lift-off angles in *Procavia* (127°) and *Galea* (125°) occur at in-phase gaits. The lowest

angle (86°) was measured in *Dasyuroides*. The coefficient of stance of the elbow joint usually is lower than the CSP of the shoulder joint; mean values fall below 0.5 in *Monodelphis*, *Dasyuroides*, *Rattus*, *Tupaia* and *Microcebus*. In *Ochotona* and *Procavia* the CSP is 0.55. Only *Galea* shows a CSP of more than 0.6 at in-phase gaits.

The range of the mean CSP of the wrist joint is similar to that of the elbow joint (Table 2A,B). The coefficient of stance in most species is below 0.5 at symmetrical gaits (0.25–0.45; *Procavia* 0.59), but it augments up to 0.36–0.65 at in-phase gaits. The mean touch-down angle of the wrist joint ranges between 168–205° at symmetrical gaits, but all species except for *Procavia* (175°) show a dorsiflexion of the wrist joint (183–202°) at in-phase gaits. *Procavia* deviates from the other species in our study by strongly reduced wrist joint excursions during the stance phase at all gaits (Fig. 2A,B). The hand is always displaced in line with the forearm owing to an anatomical restriction in the wrist joint (Fischer, 1998). The wrist joint of the other species is extended most during the last third of the stance phase, when the hand passes underneath the elbow joint. The amount of extension is much higher at symmetrical gaits (210–250°). Amplitudes of wrist joint excursion during the stance phase decreases during in-phase gaits. *Monodelphis* is the only species that extends the wrist joint to a similar degree (250°). The mean lift-off angle varies between 154° (*Tupaia*) and 215° (*Microcebus*) at symmetrical gaits and between 149° (*Tupaia*) and 227° (*Monodelphis*) at in-phase gaits.

Spine movements

Sagittal spine movements are the result of additive flexions and extensions between adjacent intervertebral joints in the lumbar vertebral column (Fischer, 1994; Fischer and Lehmann, 1998) or in the posterior thoracic and the lumbar vertebral column (Schilling and Fischer, 1999). Previous reports of a limited region of flexion and extension between Th11 and L1 in *Tupaia* (Jenkins, 1974a) have been validated only for exploratory walks (Schilling and Fischer, 1999). The additive effects of these movements lead to a displacement of the pelvis, and are called ‘pelvic movements’ in this study. Mobility within the iliosacral joint was not observed. Cranial and caudal ‘pelvic’ displacements are pronounced at in-phase gaits (Fig. 3B,C), in which the spine proves to be an important locomotory organ. Maximum cranial displacement is reached late during the swing phase and the subsequent caudal displacement continues until lift-off or even into the following swing phase. Mean touch-down angles are particular high in tail-less species, showing a nearly vertical pelvic position (e.g. *Procavia*, *Ochotona*). These angles are lower in the tailed animals (e.g. *Monodelphis*, *Tupaia*). At lift-off, the pelvis of tailed species is almost horizontal whereas in tail-less animals the pelvis is more inclined. So, tail-less species start at a more inclined position at the end of stance and reach an almost vertical position at the end of the swing, whereas species with rather long tails approach a horizontal position at lift-off but start much less inclined at stance (Fig. 4). The tail-less species

Galea, however, behaves like the two latter ones. Despite having different touch-down and lift-off angles, the effective angular movement (about 40°) is comparable between all species, except for *Ochotona*, which is more than 10° lower (Table 3B,C). The mean amplitude of the ‘pelvic movement’ during the stance phase is also lowest in *Ochotona* and highest in *Procavia*.

At symmetrical gaits, two additional ‘pelvic movements’ occur. The first, a rotation about the dorsoventral axis, is caused by lateral additive intervertebral joint movements (‘lateral bending’; Jenkins and Camazine, 1977). The second is a rotation about the longitudinal axis (‘tilting’; Jenkins and Camazine, 1977). Because of the angle’s projection into the sagittal plane, estimates of lateral bending and tilting are difficult and were not attempted here. Sagittal spine movements result in a low mean EAD of 3° and a mean amplitude of 12° for all species at symmetrical gaits. The pelvis is held virtually stable during locomotion (Fig. 3A). Pelvic position is inclined the most in *Procavia* (51° at touch-down and 47° at lift-off) and more horizontal in *Tupaia* and *Galea* (19° to 16°, and 22° to 19°). Mean pelvic angles of all other species are in the order of 35° at touch-down and 32° at lift-off.

Hindlimb

Kinematics of hindlimb segments

As in the forelimb, retraction of all hindlimb segments starts before touch-down in the last third of the swing phase at symmetrical and in-phase gaits. In particular ‘pelvic retraction’ at in-phase gaits also starts at the beginning of the stance phase and continues until the first quarter of the swing phase in trailing and leading limbs of all species (but only the leading limb of *Procavia*). Femoral retraction at symmetrical gaits ends after 95% of the stance duration (*Microcebus*), at lift-off (*Tupaia*, *Rattus*, *Procavia*) or during the first 10% of the swing phase (*Monodelphis*, *Dasyuroides*) (Fig. 3A). At in-phase gaits, femoral retraction is finished at lift-off or during the first 15% of the swing phase in trailing and leading limbs of all species. Only in *Ochotona*, does retraction of the thigh start before lift-off. In all species, protraction of the lower leg begins during the first 35% of the swing phase in both trailing and leading limbs; in *Procavia*, however, it begins in the late stance phase. At symmetrical gaits, lower leg retraction ends between 20–40% of the swing phase in all species. Although retraction of the foot comes to an end in the first third of the swing phase in trailing and leading limbs of most species, but ends at the lift-off in *Procavia* and in the late stance phase in the trailing limb of *Ochotona*. Foot protraction starts in the first third of swing phase in all species at symmetrical gaits.

Protraction and retraction of the hindlimb is executed mainly by femoral displacements at symmetrical gaits but by sagittal spine movements at in-phase gaits. At touch-down, the thigh is in an almost horizontal position in all species and at all gaits (7° at symmetrical gaits, –2° in trailing limb and –6° in leading limb at in-phase gaits). In species for which we have data for symmetrical and in-phase gaits, mean touch-

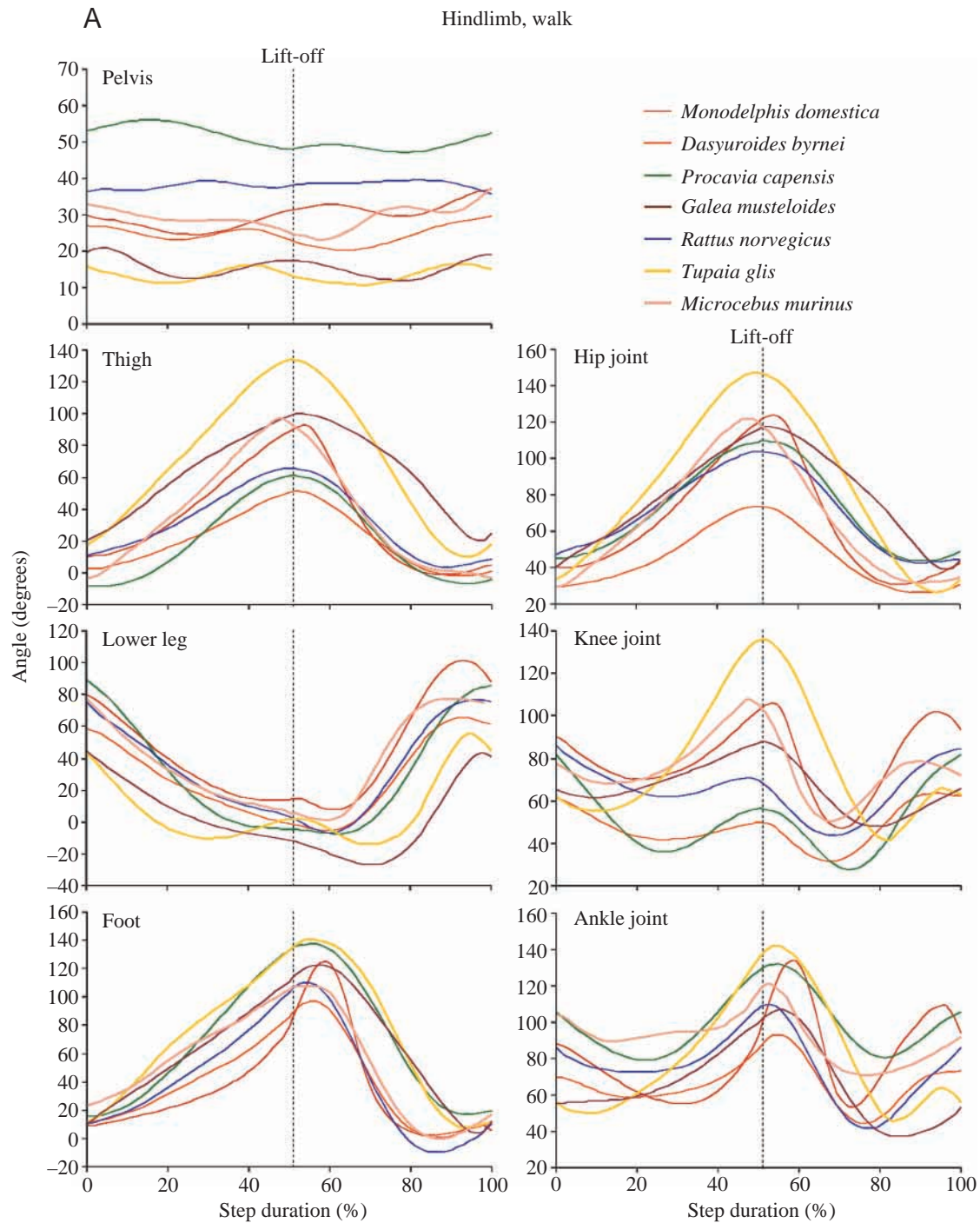
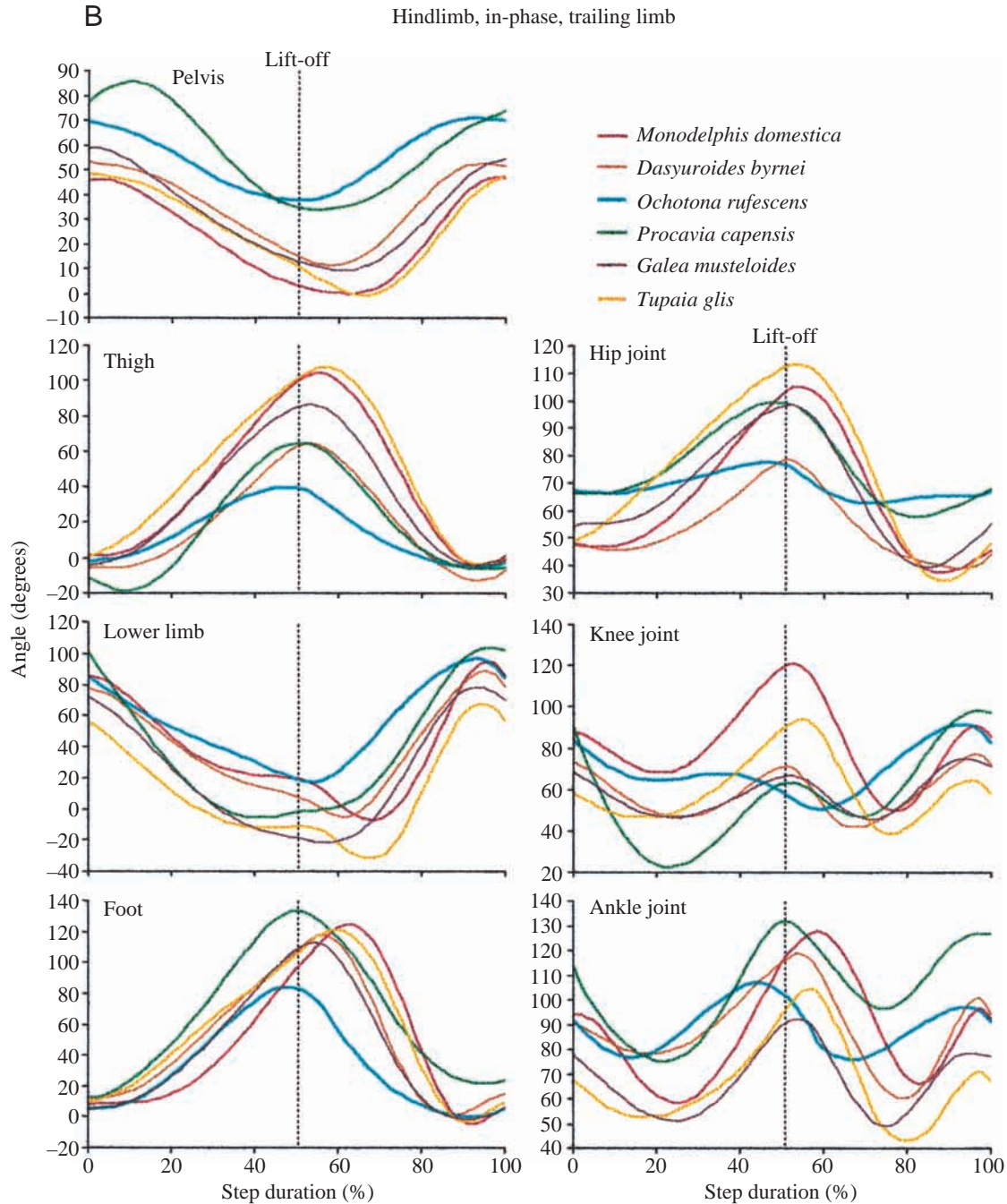


Fig. 3. Mean values of hindlimb segment angular excursions of typical sequences at symmetrical (A) and for trailing (B) and leading (C) limbs at in-phase gaits (see Fig. 2).

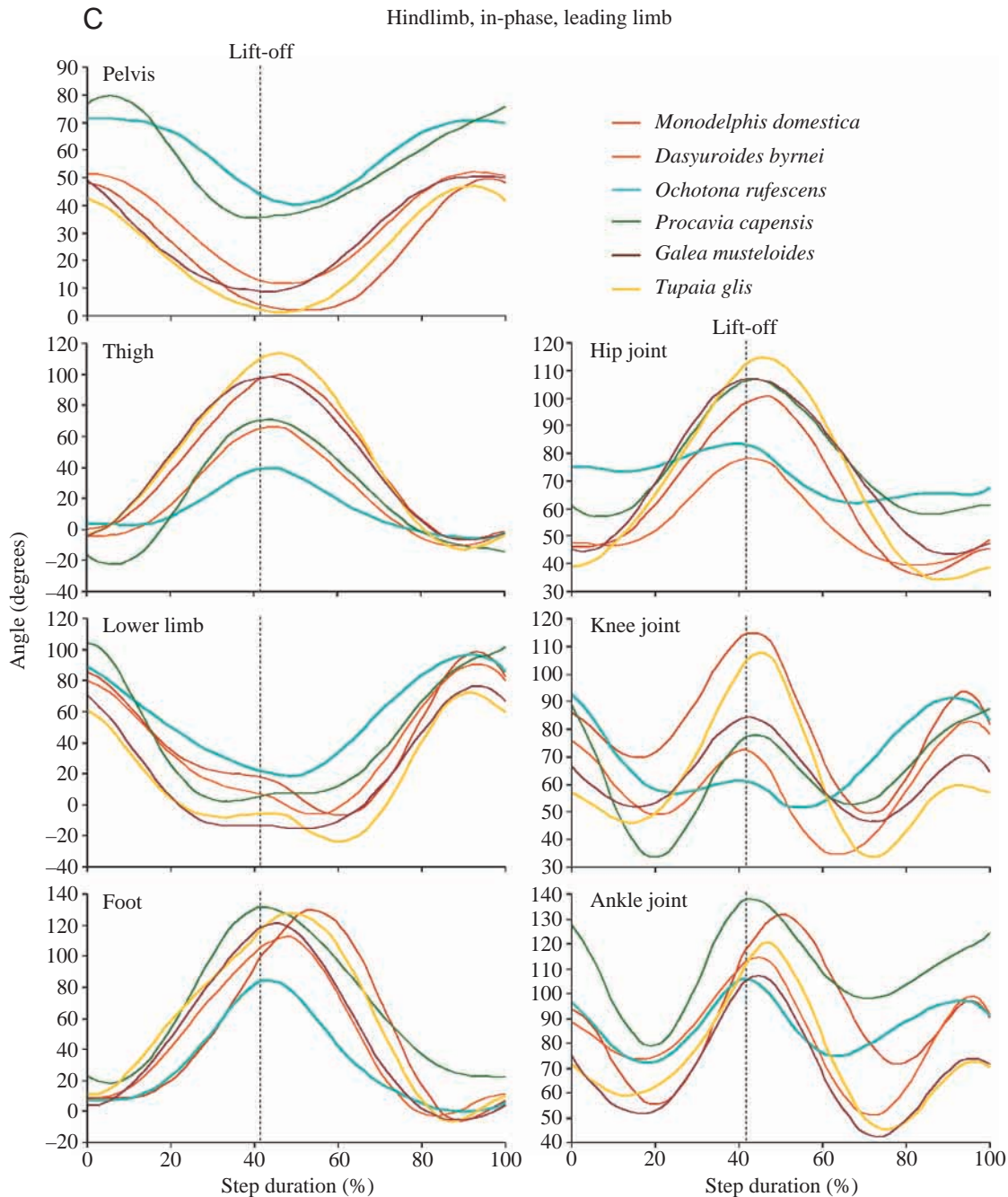
down angles at in-phase gaits decrease to positions inclined above the horizontal. Fig. 4 illustrates the highly uniform thigh position that occurs, particularly at in-phase gaits. In comparison to touch-down, mean lift-off angles are more variable ranging from 51° in *Dasyuroides* and 125° in *Tupaia* at symmetrical gaits, as well as 47° and 101° in the trailing limb and 52° and 109° in the leading limb of *Ochotona* and *Tupaia* at in-phase gaits. The femoral

retraction that follows ends with the maximum angle at lift-off or in the first part of the swing phase. Mean amplitudes of femoral displacement increase from symmetrical to in-phase gaits in all species (except *Tupaia*) and are higher in the leading limbs than in the trailing limbs at in-phase gaits. The same mean amplitudes of both hindlimbs were only observed in *Monodelphis* at in-phase gaits, because animals performed half-bound gaits.



At symmetrical gaits, the lower leg is in almost vertical at touch-down in *Microcebus*, *Procavia*, *Monodelphis* and *Rattus*, but more caudally inclined in *Dasyuroides*, *Tupaia* and *Galea* (Fig. 4). From symmetrical gaits to in-phase gaits, mean touch-down angles increase in all species. At in-phase gaits, a nearly vertical position of the lower leg is realised in *Monodelphis*, *Dasyuroides* and *Ochotona*. Differences in this touch-down position were measured in *Galea* and *Tupaia* (which show a more posteriorly inclined lower leg) and in *Procavia* (in which the lower leg is more anteriorly directed in both trailing and leading limbs). In general, mean touch-down angles are comparable between trailing and leading limbs

(Table 3B,C). The lower leg is retracted during the stance phase and reaches a horizontal orientation at lift-off (mean 1° at symmetrical gaits, 3° in trailing and 7° in leading limbs at in-phase gaits). In some species, the minimum angle of the lower leg is observed during the stance phase and afterwards the angle increases until lift-off by retraction of the foot at the end of stance. This biphasic motion of the shank (i.e. with two minima during one step cycle) is most pronounced in *Tupaia* at all gaits (Fig. 3A–C). Lower leg retraction reaches its maximum during the swing phase in all species at symmetrical gaits and in most species at in-phase gaits. Mean amplitudes are higher in all species at in-phase gaits than at symmetrical



gaits, but are comparable in *Monodelphis*. Mean amplitudes of trailing and leading limbs are nearly the same in all species.

The foot is in matched motion with the thigh, seen in particular during the stance phase at all gaits (Fig. 3A–C). Mean touch-down angles of all species occur over a small range of 4–19° at all gaits. As the foot is brought down, it is in a semidigitigrad position in all species, with the most erected foot seen in *Procavia*. The foot is in retraction and crosses its vertical position in all species during the stance phase at all gaits. Mean lift-off angle is variable at different gaits, ranging between 92° and 138° (*Dasyuroides* and *Tupaia*) at symmetrical gaits, 78–121° in trailing limbs and 81–126° in

leading limbs (*Ochotona* and *Procavia*) at in-phase gaits. Foot retraction is more restricted at in-phase gaits than at symmetrical gaits in all species (except *Dasyuroides*). After reaching its maximum retraction, the foot is protracted during the swing phase and the following retraction starts just before the next touch-down. Mean amplitudes of all species are highest at symmetrical gaits (104°), slightly lower in the leading limb (101°), and lowest in the trailing limb at in-phase gaits (99°).

Contribution of hindlimb segment movements to step length

Whereas the femur is the most propulsive segment at

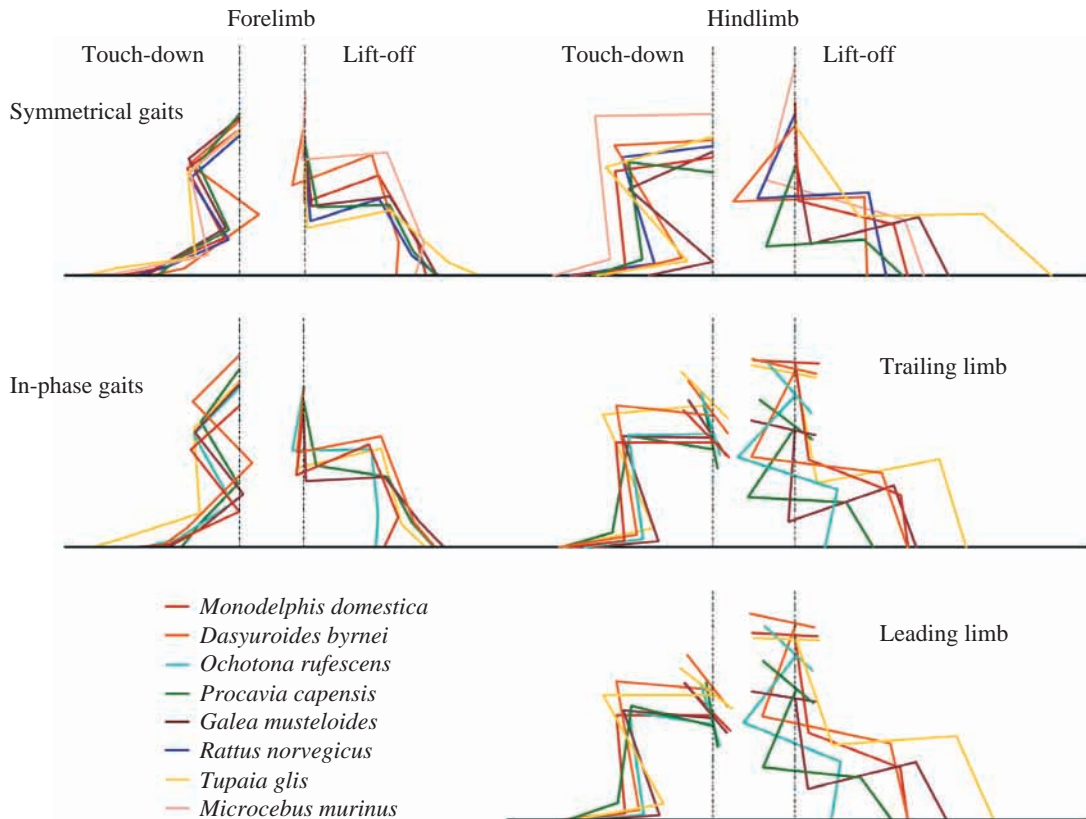


Fig. 4. Mean joint angles at touch-down and lift-off, illustrated as schematic fore- and hindlimb configurations considering limb proportions of all species under study (see Table 4) at symmetrical and in-phase gaits. Note the high uniform limb position at touch-down in contrast to that at lift-off and the more variable lift-off configuration of hindlimbs in comparison to forelimbs.

symmetrical gaits with a mean contribution of 76% to step length in all species, 'pelvic movements' contribute to half of the step length at in-phase gaits (Table 3A–C). At symmetrical gaits, the contribution of 'pelvic movements' is in the same low order as amplitudes for all species ranging between –3% and 7%. The highest value was found in *Microcebus* (10%). At in-phase gaits, the contribution of 'pelvic movement' to step length is similar in all species because the same effective angular displacement of the pelvis occurs in species with and without tails. Values are also comparable for trailing and leading limbs in most species. The only differences observed were in *Galea* and *Ochotona*, where the contribution of 'pelvic movements' to trailing limbs is higher than to the leading limbs in *Galea* and the reverse is true for *Ochotona* (Table 3B,C). Displacement of the thigh at in-phase gaits contributes to about one third of the step length, but these data are highly variable between different species. The lowest values for contribution of thigh displacement to body forward movement were found in *Ochotona* (which also showed the lowest EAD) with only 8% in the trailing and 10% in the leading limbs. The highest values of EAD, which resulted in higher contributions to step length, were observed in *Tupaia* (46% in trailing limbs and 53% in leading limbs). Comparable values were calculated for more distal segments for hindlimbs at symmetrical gaits and for trailing and leading limbs at in-phase gaits. In general, the

foot contributes more to step length (18% at symmetrical gaits and about 12% at in-phase gaits) than the shank (3% at symmetrical gaits, 9% in trailing and 4% in leading limb at in-phase gaits). The reverse case, in which the contribution of shank movements exceeds the contribution of foot movements was found only for *Ochotona* and *Procavia* at in-phase gaits and for *Procavia* and *Rattus* at symmetrical gaits.

Kinematics of hindlimb joints

In general, flexion and extension of all hindlimb joints are more pronounced during symmetrical gaits than during in-phase gaits (Fig. 3A–C). Comparisons of the limb joint behaviour of all species at in-phase gaits point to *Ochotona* as the species with the most restricted angular excursions and to *Tupaia* as the species with most extensive angular excursions. A biphasic angular movement, including one flexion and one extension per each stance and each swing phase, was found for knee and ankle joints in all species at all gaits. In contrast, hip joints show a monophasic behaviour at symmetrical and in-phase gaits, meaning that extension enters into a short plateau during the first 20% of stance at in-phase gaits (with the exception of *Tupaia*). At symmetrical gaits, the extension of the hip joint starts shortly before touch-down (80–95% of duration of the previous step cycle). There, it lasts until 90% of the stance phase in *Microcebus* and *Tupaia*, until 10% of

the swing phase in *Monodelphis* and until lift-off in all other species. At in-phase gaits, extension reaches its maximum before lift-off of the trailing limb of *Procavia* and *Ochotona*, at lift-off in *Dasyuroides* and after lift-off in all other species. Maximum angular extension of the hip joint in leading limbs occurs after lift-off in all species, but ends at lift-off in *Ochotona*.

The knee flexes before touch-down in all species at all gaits and reaches its maximum flexion at mid-stance when the foot passes underneath the hip joint. Knee joint extension, however, starts at different times at the end of stance. Knee joint extension ends independently from gaits in only two species; at lift-off in *Dasyuroides* and after lift-off in *Monodelphis*. Knee joint flexion at symmetrical gaits starts before lift-off in *Rattus* and *Microcebus* and at lift-off in *Tupaia*, *Galea*, and *Procavia*. At in-phase gaits, extension ends at lift-off in trailing and leading limbs of *Galea* and after lift-off in *Tupaia* and *Procavia*. In *Ochotona*, knee joint flexion starts earlier in trailing than in leading limbs.

The stance phase extension of the ankle joint continues into the subsequent swing phase in all species at symmetrical gaits. In most of the species, no major changes in timing were observed during the change from symmetrical to in-phase gaits. In *Ochotona*, in which only in-phase gaits were analysed, flexion starts before lift-off in trailing and in leading limbs.

The highest CSP has the hip joint in all species indicating a high degree of horizontal versus vertical action (Table 3A–C). Values within species are higher at symmetrical gaits than at in-phase gaits. With a mean touch-down angle of 40° in all species, the hip joint is flexed more at symmetrical gaits than at in-phase gaits (56° in trailing and 50° in leading limbs). Whereas hip joint angles at touch-down are similar in trailing and leading limbs of *Monodelphis* and *Dasyuroides*, they are higher in the trailing than in the leading limbs in all other species.

The range of mean touch-down angles for all species at in-phase gaits is twice that of symmetrical gaits, but is higher at symmetrical gaits than at in-phase gaits for mean lift-off hip joint angle. The lowest mean value of the hip joint at lift-off was found in *Dasyuroides* (73–80°) and the highest value in *Tupaia* (110–141°) at all gaits. Mean (\pm S.D.; lift-off angles of all species under study are 111 \pm 21° at symmetrical gaits, 96 \pm 11° in the trailing limb and 100 \pm 11° in the leading limb at in-phase gaits. At lift-off, the hip joint of the leading limb is extended more than that of the trailing limb in *Dasyuroides*, *Galea* and *Procavia* and is nearly the same in both hindlimbs in the other species. Mean lift-off angle decreases with the change from symmetrical to in-phase gaits in most species, but is comparable between both gaits in *Procavia* and lower at symmetrical than at in-phase gaits in *Dasyuroides*. Owing to the higher values at touch-down and lower values at lift-off for in-phase gaits compared to symmetrical gaits, EAD is reduced at in-phase gaits. Mean maximum angular movement amounts to 75° at symmetrical gaits, to 45° in trailing limbs and to 54° in leading limbs at in-phase gaits in all species. The highest overall amplitudes were observed in *Tupaia* (110°) at

symmetrical gaits and the lowest in the trailing limb of *Ochotona* at in-phase gaits (26°).

Discussion

Limb configuration at touch-down

The uniform forelimb configuration at touch-down is characterised by a highly consistent scapular orientation at approximately the same angle at all gaits (in all species 41 \pm 5° at symmetrical gaits, 47 \pm 4° at in-phase, mean \pm S.D.). At touch-down the relative height of the scapular pivot is equal during symmetrical gaits but spreads more widely at in-phase gaits. This reflects different elevations of the trunk. In addition, the forearm (which is in matched motion with the scapula), has a rather low range of touch-down angles. The elbow joint approximates a rectangular configuration at symmetrical gaits (86 \pm 8°), but is more extended at in-phase gaits (94 \pm 10°). The wider range of the shoulder joint and the humeral position (S.D. of both 14–17°) is mainly due to the stronger extension in *Tupaia* and *Microcebus*, and stronger flexion in *Dasyuroides*. Together with the relatively longer forearm, which contributes to the overall limb length (Table 4), this leads to the most anterior touch-down position in *Tupaia* and *Microcebus* (Fig. 4). The touch-down position of *Dasyuroides* is within the range of the other mammals despite the stronger shoulder joint flexion. Within each species, the touch-down point is at a constant distance from the perpendicular of the scapular pivot, just below the eye. Increases in step length are due to a more posterior transition of the lift-off point.

Observations on forelimb movement of the walking *Didelphis marsupialis* (Jenkins and Weijjs, 1979) correspond to those of our small mammals. In *Didelphis*, scapular angle at touch-down ranges between 40–50° and the humerus is oriented almost vertically. Shoulder and elbow joints are extended approximately 130° and 110°. The touch-down position of the forelimb in *Cavia porcellus* (Rocha Barbosa et al., 1996) is very similar to that of its near relative *Galea* at all gaits. In the case of exploratory walking in *Rattus norvegicus* (Jenkins, 1974b), overall forelimb excursions are reduced and the point of touch-down lies slightly ahead of a point directly beneath the shoulder joint. In this case scapular touch-down angle is higher (50–60°) and humeral angle is smaller (45°) in exploratory walking compared to moderate walking. Limb kinematics were documented cineradiographically for a series of small mammals by Jenkins (1971). Differences in humeral touch-down angles and positions of touch-down points between the species studied by Jenkins and our sample of small mammals are probably caused by the slow speed of the exploratory walk investigated by Jenkins.

In *Felis catus* f. *domestica*, the forelimb is more extended at touch-down than in our animals. Whereas the scapular angle measured in cineradiographic studies is the same as in our species (40–46°; Boczek-Funcke et al., 1996), shoulder and elbow joint angles are about 30° higher. Scapular touch-down angles obtained in *Felis* (using externally applied markers) amount to 40–50° (Miller and Van der Meché, 1975; English,

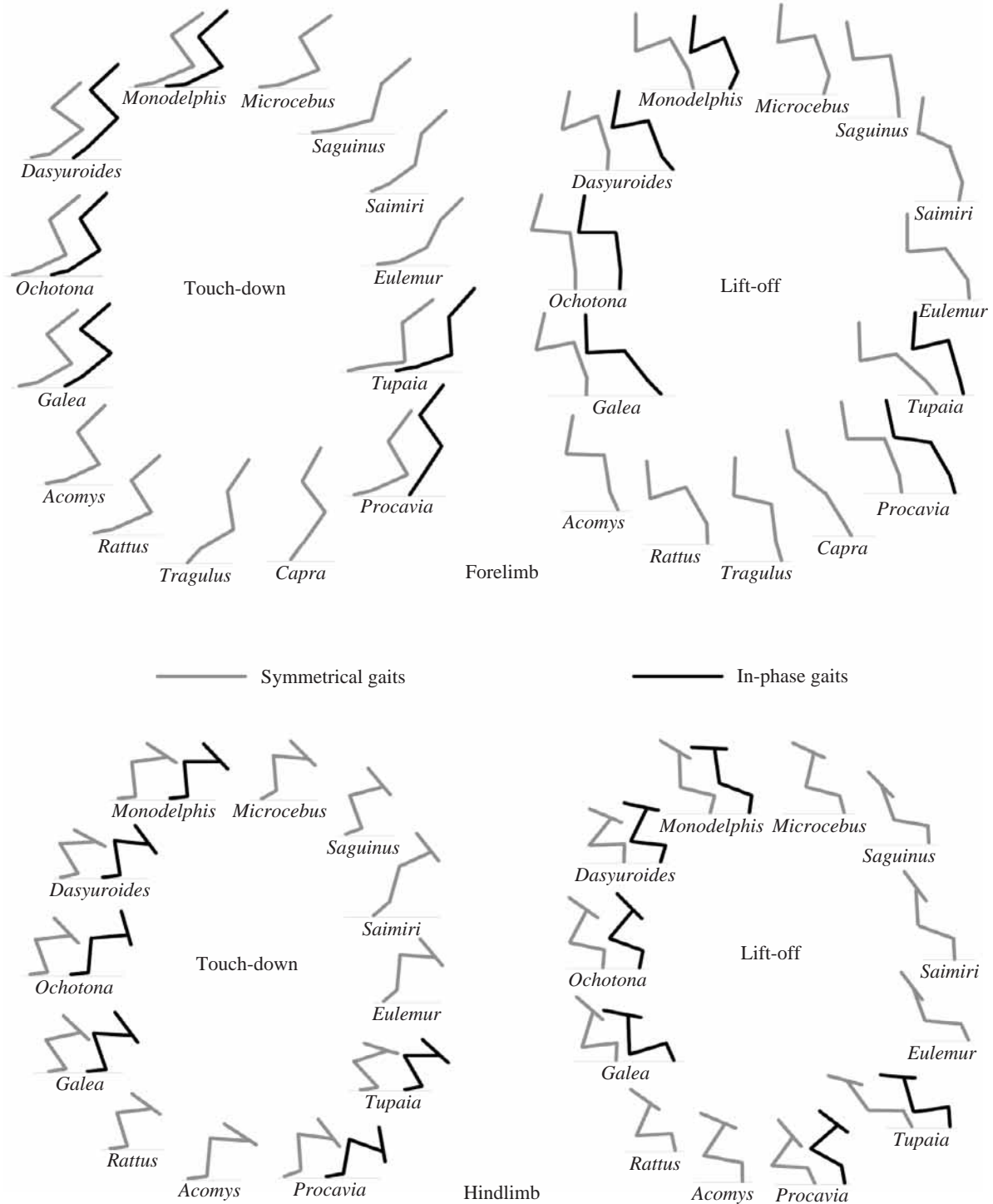


Fig. 5. Schemes of limb configurations at touch-down and lift-off in 14 species at symmetrical (grey) and in-phase gaits (black). Limb proportions are set into the same ratios to emphasize the overall kinematic pattern.

1978; Halbertsma, 1983). In primates, forelimb posture at touch-down is characterised by an increasing amount of extension in the shoulder and elbow joints, which together with proportional changes between forelimb segments, results in a cranial displacement of the touch-down point (Jouffroy et al., 1983; Larson et al., 2000; Schmidt and Fischer, 2000). With

increasing body size in arboreal-quadrupedal primates the forelimb protraction augments (Schmidt and Voges, 2001). Cineradiographic studies of shoulder movements in primates indicate that the amount of scapular rotation is reduced in larger species by both a higher touch-down angle (57° in *Cercopithecus aethiops*: Whitehead and Larson, 1994; 49° in

Eulemur fulvus: Schmidt and Fischer, 2000) and a lower lift-off angle. Only *Capra hircus*, the domestic goat, deviates clearly from other mammals in having a more extended limb, with shoulder joint angles of more than 135° and elbow joint angles of 120° (Lilje and Fischer, 2001). Scapular retraction starts at an angle of 61° in *Capra* and 56° in *Tragulus javanicus* (the mouse deer; unpublished data) (Fig. 5).

Whereas the forelimbs show no fundamental geometrical differences between symmetrical gaits and in-phase gaits, in that three segments are always displaced, hindlimb protraction is also executed by three hindlimb segments at symmetrical gaits. At in-phase gaits, intervertebral lower spine movements (causing a sagittal 'pelvic displacement') act functionally as an additional fourth segment. Despite this, femoral position is comparable at all gaits being almost horizontal at touch-down (in all species = 7±10° at symmetrical gaits, -2±5° in trailing limbs and -6±5° in leading limbs at in-phase gaits; means ± S.D.). This position is achieved by hip joint movement at symmetrical gaits, but is mainly passively induced by sagittal spine flexion (and to a lesser degree to hip joint flexion) at in-phase gaits. As occurs in the forelimb, the distal segment is in matched motion with the femur. The foot is in the same position (S.D. ≤5°) 12° at symmetrical gaits, 10° in trailing limbs and 9° in leading limbs at in-phase gaits. At symmetrical gaits, hip joints of all species have relatively similar positions at touch-down, indicated by a relative low value of S.D. (40±5°). The knee joint, however, shows a little more variation (75±12°) and the ankle joint is the most variable (80±20°). Standard deviations increase in hip joints (56±12° in trailing limbs and 50±10° in leading limbs) whereas they are nearly constant, or decrease, in knee joints (77±11° resp. 75±6°) and ankle joints (89±16° resp. 87±14°) at in-phase gaits.

Quantitative data on sagittal pelvic displacement are available for *Cavia* at trot and gallop (Rocha Barbosa et al., 1996). Its touch-down angle of 28° is similar to *Galea* and the two metatherians at symmetrical gaits. The high value of 70° at gallop corresponds to the data of tailless species in our sample. Gasc (1993) described hindlimb kinematics in the tailed rodent *Meriones shawi* at gallop. Although pelvic displacement was not quantified, angles at touch-down and lift-off can be estimated from a stick-figure drawing. Touch-down angles in *Meriones* are approximately 34° for trailing limbs and 32° for leading limbs and are always smaller than values measured in our tailed species. The pelvis touch-down angle of the walking *Mephitis mephitis* was also estimated from a stick-figure drawing (45°; Van de Graaff et al., 1982) and lies in the range of our observations.

Descriptions of hindlimb movements are available for a series of small to medium sized mammals. The touch-down position of the thigh in *Didelphis*, *Tupaia*, *Mustela putorius* (ferret), *Mesocricetus auratus* (hamster), *Heterohyrax brucei* (hyrax), and *Rattus* is more or less horizontal (Jenkins, 1971), and corresponds to angles reported here. The same is true for the *Cavia* (Rocha Barbosa et al., 1996) and for both trailing and leading limbs in the galloping *Meriones* (Gasc, 1993). As observed by Jenkins and Camazine (1977), the thigh is

protracted at an angle of 30° below the horizontal line in *Felis*, *Vulpes fulva* (the fox) and *Procyon lotor* (the racoon) at touch-down. The highest mean touch-down angle of the thigh (51°) is given for *Mephitis* by Van de Graaff et al. (1982). The more retracted thigh in *Felis* (Kuhtz-Buschbeck et al., 1994) and *Mephitis* reflects a more extended limb with higher extension of both hip joint (65° and 97°, respectively, in comparison to our sample mean 43°) and knee joint (120° and 154–73°). The ankle joint angles are also more extended, being approximately 30° in *Felis* (Kuhtz-Buschbeck et al., 1994) and 60° in *Mephitis* (Van de Graaff et al., 1982).

Limb configuration at lift-off

Limb configuration of the forelimb at lift-off consists of a vertically placed scapula (in all species 92±7° at symmetrical gaits, 87±9° at in-phase; means ± S.D.) and a nearly horizontally placed humerus, especially at in-phase gaits (-13±7° respectively -2±9°). The scapula initiates lift-off (Roberts, 1974), more or less waiting the last 20% of the stance phase for the other joints to take off. The actual lifting off is caused by a strong flexion in the elbow. It is interesting to note that elbow extension decreases with increasing speed at walk and slow trot but increases with increasing speed at in-phase gaits (Fischer, 1998; Fischer and Lehmann, 1998; Schilling and Fischer, 1999; Schmidt and Fischer, 2000).

The mean (±S.D.) lift-off angle of the pelvis (30±11°) compared to that at touch-down (33±11°) indicates that only minor 'pelvic movements' occur at symmetrical gaits. Lower mean values for pelvic lift-off position, in the leading compared to trailing limbs, is caused by the ongoing sagittal extension during stance (18±18° versus 21±18°). In comparison to limb configuration at touch-down, hindlimb position at lift-off is more variable among all species, especially in the knee joint, caused by differences in retraction excursions of the thigh. Knee joint and thigh lift-off position are more variable between all species at symmetrical gaits (83±27°, 81±26°) than in trailing limbs (78±23°, 75±23°) and leading limbs (87±17°, 82±22°) at in-phase gaits. Hindlimb configuration at lift-off is marked by a horizontal positioning of the shank at all gaits (in all species = 1±11° at symmetrical gaits, 3±16° in trailing limbs and 7±14° in leading limbs at in-phase gaits; means ± S.D.).

The pelvis in *Mephitis* is in a more inclined position at touch-down and at lift-off at symmetrical gaits (38°; Van de Graaff et al., 1982) indicating a more inclined position in general in comparison to data presented here (30°). Effective angular movement of the pelvis is a little bit higher in *Cavia* (12°; Rocha Barbosa et al., 1996) than in *Galea* (3°), but the amplitude (10°) is comparable. The more extended limb configuration in *Felis* and *Mephitis* at symmetrical gaits is also represented in lift-off positions of hindlimb joints. At mean lift-off angles in hip and knee joints of 130° in *Felis* (Kuhtz-Buschbeck et al., 1994) and of 163° and 149°, respectively, in *Mephitis* (Van de Graaff et al., 1982), all of these values are clearly higher than those of the species we studied (111°, 83°). Ankle joint angles at lift-off augment with increasing speed in

Felis (113–146°; Kuhtz-Buschbeck et al., 1994) and are comparable at lower speeds (0.33–1.19 m s⁻¹) to the mean angle we observed (115°). In comparison, the ankle joint is more flexed at lift-off in *Mephitis* (i.e. 84° at 0.28 m s⁻¹; Van de Graaff et al., 1982).

At in-phase gaits, femoral retraction of the trailing limb in the species studied here (47–109°) range between values for *Meriones* (60°; Gasc, 1993) and *Cavia* (90°; Rocha Barbosa et al., 1996). Values for *Galea* (mean 86°) investigated here are comparable to those for *Cavia* (90°; Rocha Barbosa et al., 1996) indicating a nearly vertical position. Overall, the more inclined pelvic position in *Cavia* at in-phase gaits (Rocha Barbosa et al., 1996), indicates that pelvic positioning is similar to other tailless species studied here, except *Galea*. However, amplitudes and effective angular movements are comparable between both caviids. As in our tailed species, the pelvis is also oriented very near to the horizontal at lift-off in *Meriones* (6° for trailing and 9° for leading limbs; Gasc, 1993). The hip joint in the trailing limb is flexed most at lift-off in *Meriones* (65°, Gasc; 1993), extended a little bit more in the species included in our study (mean 96°, range 93–112°) and extended most in *Cavia* (115°; Rocha Barbosa et al., 1996). As in the hip joint, the knee joint is also flexed more in *Meriones* (51°; Gasc, 1993) than in our species (59–119°) or in *Cavia* (100°; Rocha Barbosa et al., 1996). As far as the ankle joint is concerned, values for both *Meriones* (119°; Gasc, 1993) and *Cavia* (107°; Rocha Barbosa et al., 1996) are well within the range of values reported here (91° to 125°).

Amplitudes during stance phase

Differences between symmetrical and in-phase gaits, observed in all joints, point to more elevated limbs in the latter gaits (Fig. 5, Tables 2A,B, 3A–C). As the extended position is held throughout the stance and flexion reduced, especially at midstance, all amplitudes of limb joints decrease during the transition from symmetrical to in-phase gaits in all species we studied.

Scapular amplitudes range between 44° (*Dasyuroides*) and 60° (*Galea* and *Rattus*) during the stance phase at symmetrical gaits. These amplitudes are reduced at in-phase gaits, ranging from 37° to 48°. Previously published values on scapular rotation in walking *Rattus* collected from cineradiography are lower than those measured here by approximately 15° (Jenkins, 1974b, but see our earlier remarks on slow exploratory walk). In *Didelphis*, scapular rotation amounts to 40° at a slow walk or to 50° at a fast walk (Jenkins and Weijs, 1979). The amplitudes of scapular rotation in *Cavia* deviate from those of our species by having higher values at both symmetrical (trot: 62°) and in-phase gaits (gallop: 70°), caused mainly by an extraordinary high angle at lift-off (107–115°). Scapular amplitudes range from 38° (walk) to 42° (trot and gallop) in *Felis* (English, 1978b). Whereas the values for the walking *Felis* have been confirmed by a later cineradiographic study (40°; see Boczek-Funcke et al., 1996), scapular rotation is

underestimated in trotting *Felis* (58°; Sontag and Cremer, 1978), most probably due to the external registration techniques of English's study.

Published data on shoulder joint amplitudes are in accordance with our observations. While maximum amplitudes during stance are relatively low in *Felis* (24–28°; Boczek-Funcke et al., 1996), observations in *Didelphis* (35–45°; Jenkins and Weijs, 1979) and *Cavia* (46° at symmetrical and 35° at in-phase gaits; Rocha Barbosa et al., 1996) are close to ours. The amplitudes of elbow joint excursions during the stance phase in *Felis* (41°), *Didelphis* (40°) and *Cavia* (42°) at symmetrical gaits, lie within the same small range as in the species analysed in this study. The digitigrad *Felis* resembles the digitigrad *Procyon* in overall behaviour of the wrist joint (Caliebe et al., 1991; Miller and Van der Meché, 1975) inasmuch as amplitudes are relatively low, especially with increasing speed and dorsiflexion is restricted.

Amplitudes of 'pelvic movements' are highly comparable between all species under study indicated by low standard deviations at symmetrical (3°) and at in-phase gaits (8° in trailing and 5° in leading limbs). The mean amplitude of 'pelvic movements' for all species in the current study is 12° at symmetrical gaits, the same as reported for *Cavia* (Rocha Barbosa et al., 1996). At in-phase gaits, the mean amplitudes of 'pelvic movements' range between 27° and 49° in trailing limbs and between 31° and 46° in leading limbs. The value for the trailing limb in *Cavia* is within the range given here (48°; Rocha Barbosa et al., 1996) and is only a little bit higher than the mean value observed for *Galea* (44°). The amplitude of thigh movements in the species studied here (during the stance phase at symmetrical gaits) ranges between 51° (*Dasyuroides*) and 84° (*Monodelphis*) in most species and is higher only in *Tupaia* (110°). Values given by Jenkins and Camazine (1977) for *Vulpes*, *Mephitis* and *Felis* (63°, 72° and 72° respectively) are in-between the range we observed. For in-phase gaits, data for femoral amplitudes at stance phase are only available for the trailing limb in *Cavia* (48°; Rocha Barbosa et al., 1996) and for the leading limb in *Meriones* (70°; Gasc, 1993). These values are comparable to those reported here, which range between 50° (*Ochotona*) and 98° (*Monodelphis*) in the trailing limbs and between 61° (*Ochotona*) and 109° (*Tupaia*) in the leading limbs. Whereas mean hip joint and knee joint amplitudes are comparable to each other at in-phase gaits (45° and 43° in trailing limbs and 54° and 44° in leading limbs), hip joint amplitude in the current study is twice as high as knee joint amplitude at symmetrical gaits (75° and 38° respectively). Hip and knee joint amplitudes are clearly different at all gaits in *Cavia* being 63° and 25° at trot and 63° and 35° in the trailing limb at in-phase gaits (Rocha Barbosa et al., 1996). A remarkable decrease in the mean amplitude occurs in the ankle joint of *Cavia* during the change from symmetrical (80°) to in-phase gaits (17° in trailing limb) (Rocha Barbosa et al., 1996). The mean amplitude of the trailing limb in *Cavia* falls short of the range observed here (35° in *Ochotona* and 74° in *Monodelphis*), but the value for ankle joint amplitude at

symmetrical gaits is in between the range we found (36° in *Microcebus* and 88° in *Tupaia*).

To summarize, kinematics accompanying the transition from symmetrical to in-phase gaits offer no uniform pattern as implied by earlier studies, which discussed reduced joint amplitudes at in-phase gaits compared to symmetrical gaits. Studies of the majority of limb joints in *Procavia* (Fischer, 1994) or of the shoulder joint in *Cavia* (Rocha Barbosa et al., 1996) suggested that angular movements at in-phase gaits were reduced, but there is no species-independent, single pattern that accompanies the transition from symmetrical to in-phase gaits. In the case of scapular movements and hip joint angular movements, amplitudes decreased in all of our species at in-phase gaits. In *Cavia*, however, scapular displacements increased and hip joint angular movements remained constant (Rocha Barbosa et al., 1996). Whereas amplitudes decrease during the change from symmetrical to in-phase gaits in the shoulder joints of *Procavia*, *Monodelphis*, and *Cavia* (Rocha Barbosa et al., 1996), they increase in *Galea* and remain constant in *Dasyuroides* and *Tupaia*. Elbow joint excursions increase at in-phase gaits in *Monodelphis* and *Galea* and decrease in all other species. Wrist joint angular movements are more pronounced at symmetrical gaits than at in-phase gaits in *Monodelphis*, *Dasyuroides* and *Tupaia*. The reverse is true for *Procavia*, *Galea*, and *Cavia* (Rocha Barbosa et al., 1996). In the hindlimb, knee joint amplitudes decrease at in-phase gaits only in *Tupaia* and increase in all other species, including *Cavia* (Rocha Barbosa et al., 1996), but are constant in *Galea*. Ankle joint amplitudes at in-phase gaits are only one quarter as high as at symmetrical gaits in *Cavia* (Rocha Barbosa et al., 1996). Although not as dramatic as in *Cavia*, decreases are also observed for ankle joint amplitudes in *Galea* and *Tupaia*, while increases were observed in all of the species we studied.

Contribution of segments to step length

The 'overlay method' approach (Fischer and Lehmann, 1998) that we used to calculate the contribution of displacements of different segments to step length, explicitly considers the vertical displacement of pivots during stance. As this is the first study that compares the segment's contribution to step length, no other data outside our working group are available for comparison. Calculations indicate the predominance of scapular retraction in forelimb movement, while the contribution of humeral displacement to step length is always less than half of the scapular value. The contribution of the forearms only exceeds the value of the upper arm in species in which the forearm is extensively retracted, such as *Tupaia* at symmetrical gaits or *Galea* at in-phase gaits. Hand movements contribute to step length in most species with approximately 5% and never more than 10%.

Despite the different limb configuration of artiodactyls and the lowest amplitudes of scapular rotation observed, the contribution to step length of the most proximal segment is the highest (73%) in the goat, simply because of the high scapular pivot (Lilje and Fischer, 2001). Our calculations of the scapular

contribution does not consider translation of the scapula along the thoracic wall known from the acclavicular *Felis* (Boczek-Funcke et al., 1996) and *Procavia* (Fischer, 1998). The more extended limbs observed in most species at in-phase gaits lead to a more elevated position of the body and thus a higher scapular or elbow pivot. So the same or even higher contribution to step length can be achieved by lower effective angular movements (EADs).

As in the forelimb, analysis of the contribution of segment's movement to step length, point to the most proximal element as the most propulsive segment in the hindlimb. Because of the fundamental change in hindlimb motion between symmetrical and in-phase gaits, resulting in a different number of acting segments, distinct changes in the contributions of individual hindlimb segments occur. At symmetrical gaits, femoral protraction and retraction contribute three-quarters to step length and the remainder is mainly contributed by foot and shank movements. 'Pelvic movements' contribute only to a lesser degree. In contrast to this, the main part of body propulsion – half the step length – is contributed by additive sagittal spine movements at in-phase gaits. Despite the differences in touch-down and lift-off positions of the pelvis in tailed and tailless species, their contribution of 'pelvic movements' is comparable, owing to similar effective angular movements. One third of step length is added by thigh movement at in-phase gaits and the rest is shared by foot and shank movements.

Final conclusion

The comparison of kinematic data of different therian mammals suggests that therian mammals with small body sizes (90–2500 g) display the same overall behaviour of limb displacement during locomotion. To test this hypothesis, we included *Procavia* in our analysis, which descends most probably from larger cursorial ancestors and is secondarily dwarfed (Thenius, 1979; Fischer, 1986, 1992). *Tragulus*, the smallest ruminant, also supports the hypothesis that mainly body size constraints the kinematic pattern (Fig. 5).

In general, kinematics of small therian mammals are obviously independent of their systematic position (at least in species selected here), of their natural habitat (when we accept that kinematics on the treadmill parallels unrestrained kinematics), and also of specific anatomical dispositions. Obviously, characters such as finger or toe reduction, fusion of zygapodial elements, reduction of the clavicle, carpal or tarsal specializations, and even extreme elongation of metapodials in *Tragulus* do not affect the overall kinematic pattern of therians.

The consequences of gait change from symmetrical to in-phase gaits are strikingly different on forelimb and hindlimb. Whereas only timing changes on the forelimb (kinematics remain the same!), hindlimb kinematics change significantly. In small therian mammals, in-phase gaits are marked by an extensive sagittal bending of the lumbar spine as has been shown by cineradiography. Small intervertebral movements add up and pelvic retro- and protraction is their obvious effect (Fischer, 1994; Rocha Barbosa et al., 1996; Schilling and

Fischer, 1999). Sagittal spine movements contribute roughly one half to the total propulsive movement during stance at in-phase gaits. The occurrence or absence of a long tail influences the pelvic position at touch-down and lift-off but not the total displacement. The pelvic course of movement starts from a nearly vertical position in tailless species and at a more caudally inclined position in tailed species. It ends at a horizontal position in tailed species at lift-off and a more inclined position in tailless species (Fig. 4). We have problems interpreting the graph of the tailless *Galea* since it behaves more like a tailed species. For example, observations on *Cavia* (Rocha Barbosa et al., 1996), a sister taxon of *Galea*, show the typical pelvic course of movements as in our tailless species.

Studies on midsize carnivores (*Felis*, *Vulpes*, *Procyon*) and our data on *Capra* strongly suggest that the elevated limb position of these forms has some influence on their kinematics. Still, the three-segmented fore- and hindlimbs are displaced in the same proximal pivots as in the smaller therians, and these are situated at the same level. While the scapular displacement remains the same in *Felis*, scapular EAD is reduced in *Capra*. In contrast, the high location of the scapular pivot leads to the highest contribution to step length in this artiodactyle. As a consequence of the more extended limbs, the position of humerus, femur and shank is more inclined at the beginning and end of stance with respect to their horizontal position in small therians. As there are no cineradiographic data on midsize or even larger mammals at in-phase gaits, we cannot estimate the impact of gait change on kinematics and especially on lower spine movements.

The identification of a basically uniform pattern of kinematics in small therians leads to the suggestion, that mesozoic mammals of the therian stem lineage, which have been small to very small (Jenkins and Schaff, 1988; Krebs, 1991; Hu et al., 1997; Ji et al., 1999; Luo et al., 2001) had the same kinematic pattern. This configuration of limb segments is considered to represent the ancestral therian design of limbs with respect to other amniotes and especially monotremes (Pridmore, 1985). Its main function can be seen as an adaptation to irregularities of the ground. Such irregularities are thought to pose major handicaps for therians with parasagittal placed limbs (Fischer, 2001). Relative to small body sizes, support on ground or on off-ground strata are comparable, as has already been pointed out for *Tupaia* by Jenkins (1974a). Therefore, discussion on arboreality in small mammals seems inadequate.

In summary, basic elements of locomotion of small to midsize therians are: (1) a three-segmented limb with zigzag configuration, which is mainly displaced at the highest possible pivot; (2) position of scapular pivot and hip joint at the same height over the ground at symmetrical gaits and consecutively similar functional length of fore- and hindlimbs; the matched motion of two segments (scapula/lower arm, femur/metatarsus) during retraction of limbs; (3) kinematics of forelimbs are independent of speed and gait; (4) the fundamental change from femur retraction at symmetrical gaits to sagittal spine movement at in-phase gaits resulting in different hindlimb kinematics; (5)

propulsive movement of the body is mainly achieved by the most proximal acting limb segments (scapula and femur at symmetrical gaits, scapula and sagittal spine movements at in-phase gaits) while all further distal limb joints contribute only to a lesser degree to step length.

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