

HINDLIMB KINEMATICS DURING TERRESTRIAL LOCOMOTION IN A SALAMANDER (*DICAMPTODON TENEBROSUS*)

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Summary

A quantitative study of hindlimb kinematics during terrestrial locomotion in a non-specialized salamander was undertaken to allow comparisons with limb movements in other groups of tetrapods. Five *Dicamptodon tenebrosus* were videotaped at 200 fields s^{-1} walking on a treadmill. Coordinates of marker points on the salamander's midline, pelvic girdle and left hindlimb were digitized through at least three strides at both a walk (0.77 SVL s^{-1} , where SVL is snout–vent length) and a trot (2.90 SVL s^{-1}). Marker coordinates were used to compute kinematic variables summarizing trunk flexion, pelvic girdle rotation, femoral protraction/retraction and knee flexion/extension. The stride is characterized by uninterrupted trunk and pelvic girdle oscillation, femoral retraction throughout stance phase, and knee flexion in early stance followed by extension. Mean angular excursions are: trunk, 66° ; pelvic girdle, 38.5° ; pelvic girdle–femur, 106° ; and knee, 65° . The hindlimb and pelvic girdle also show a complicated pattern of lateral movement related to knee flexion/extension and periods of support by the contralateral hindlimb during the step cycle. *Dicamptodon* shares the following features of the hindlimb step cycle with other tetrapod taxa: rotation of the pelvic girdle through a $30\text{--}40^\circ$ arc, femoral retraction beginning simultaneously with and persisting throughout stance phase, flexion of the knee in early stance, and extension of the knee in late stance.

Introduction

Vertebrate morphologists have a long history of using salamanders as a window into the locomotor capabilities of primitive tetrapods. Howell (1944, p. 224) stated that 'The earliest tetrapods, when they emerged from an aquatic habitat, must have progressed much as does a salamander today.' In their skeletal and gross morphology, fossil primitive tetrapods more closely resemble salamanders than any other extant tetrapod group (Schaeffer, 1941; Carroll, 1988), though current understanding of tetrapod phylogeny clearly shows that modern amphibians are an offshoot lineage and not on the main branch leading to higher tetrapods (Carroll, 1988; Milner, 1988; Panchen and Smithson, 1988). Nonetheless, many researchers have examined modern salamanders in

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an attempt to identify primitive locomotor features (Romer and Byrne, 1931; Schaeffer, 1941; Howell, 1944; Gray, 1968), and this clade is still recognized as the closest approximation to the primitive tetrapod condition (Gans and De Gueudre, 1992). The other two extant lissamphibian clades, frogs and caecilians, do not possess locomotor morphologies similar to those of early tetrapods. Caecilians lack legs, while the highly modified skeleton and saltatory locomotor mode of frogs are found only in this clade (Duellman and Trueb, 1986). In contrast, modern salamanders retain several features thought to be shared by the earliest tetrapods. These characteristics include sprawling posture (generally accepted to be primitive for tetrapods; Gregory and Camp, 1918; Romer, 1922; Schaeffer, 1941; Howell, 1944; Gray, 1968; Rewcastle, 1981; Carroll, 1988) and the ability to generate undulatory waves with their axial musculature (Daan and Belterman, 1968; Gray, 1968; Frolich and Biewener, 1992). Also, the skeletal structure of the pectoral/pelvic girdles, limbs and particularly the tarsus is the closest available analogue to that of the earliest tetrapods (Schaeffer, 1941). Finally, during the stance phase of a stride, the major axis of the pes of salamanders always points forward, unlike those of many previously studied lizards (such as iguanids), whose feet point out to the side during later stance (Schaeffer, 1941; Brinkman, 1980*b*, 1981). This maintenance of pes orientation is accomplished by the long-axis rotation of the bones of the crus, with the tibia crossing in front of the fibula, much as the radius and ulna of the human forearm cross during rotation of the wrist. Fossil trackways show that the earliest terrestrial tetrapods also possessed this characteristic of the pes always pointing forward during walking (Romer and Byrne, 1931; Schaeffer, 1941).

Previous studies of salamander locomotion have ranged in subject matter from attempting to understand probable movements of labyrinthodont limbs by analyzing films of walking newts (Schaeffer, 1941) and categorizing the typical salamander gait (Hildebrand, 1966, 1976), to deriving forces exerted by the limbs (Barclay, 1946) and investigating the relationship between sensory feedback and central neural commands in the control of the forelimbs (Szekely *et al.* 1969). Edwards (1977) measured the relative contributions of girdle rotation, limb retraction and limb rotation to locomotion, and both Edwards (1977) and Gray (1968) have offered theoretical discussions of how each of these facets of limb movement can combine to produce the greatest stride length. More recently, a focus has been put on the axial locomotor system, with several studies describing lateral undulations of the body and attempting to dissect standing from travelling waves (Daan and Belterman, 1968; Sukhanov, 1974; Edwards, 1977; Frolich and Biewener, 1992). Carrier (1993) has described differential functioning of a component of the axial locomotor system, the hypaxial musculature, during swimming and walking.

In spite of this volume of work, several avenues of investigation remain unexplored. For instance, salamanders represent one of the two possible tetrapod groups in which to examine simultaneous functioning of two locomotor systems that are each believed to be independently capable of driving forward progression: lateral bending produced by the axial musculature and stepping by the limbs. It has long been known that salamanders use only symmetrical gaits (walk and trot; Hildebrand, 1976, 1985; Edwards, 1977). Asymmetrical gaits (gallop) are thought to be impossible for quadrupeds with sprawling

posture because they lack support by legs positioned directly under the body (as in mammals), a consequence of both the wide track of the feet and lateral displacements of the trunk during axial bending. Although the studies of Frolich and Biewener (1992) and Carrier (1993) have demonstrated the plasticity of the axial locomotor system in response to different physical environments, patterns of axial bending are generally treated as being stereotyped (either standing or travelling waves) and independent of limb movements (Gray, 1968; Edwards, 1977; Frolich and Biewener, 1992). To date, no attempt has been made to interrelate detailed limb movements with movements of the body (Gans and De Gueudre, 1992). Such information may illuminate possible constraints on the timing of limb protraction and retraction with phases of axial bending.

Comparative data for tetrapods also remain incomplete. While salamanders have been used as models to identify general features of primitive tetrapod locomotion (Schaeffer, 1941; Gray, 1968), quantitative kinematic data are scarce. Several authors (Gray, 1968; Edwards, 1977, 1989; Peters and Goslow, 1983) have maintained that the salamander hindlimb operates according to the 'double crank' mechanism proposed by Barclay (1946, see explanation in Fig. 10A). However, to date, no attempt has been made to describe in detail the movements of the various sections of the salamander limb, which would serve as a test of the applicability of the double crank model. Also, no data exist on the similarity of limb kinematics between salamanders and other tetrapod groups, such as lizards (Brinkman, 1981) and crocodylians (Schaeffer, 1941; Brinkman, 1980a; Gatesy, 1991), or birds (Gatesy, 1990; Johnston and Bekoff, 1992) and mammals (Goslow *et al.* 1973, 1981; Wetzel *et al.* 1976; Jenkins and Camazine, 1977; Goslow and Van De Graaff, 1982; Vilensky and Gankiewicz, 1990). Hindlimb joint angle profiles during stepping have been published for mammals and birds, but no equivalent data exist for any sprawling tetrapod. Such comparisons may offer insight into possible constraints that sprawling or upright posture may impose on kinematic patterns. Finally, comparison of step cycle variables and kinematics among tetrapod groups may reveal common features that could have been inherited from the common ancestor of all tetrapods.

Therefore, the objectives of this study are to describe in detail the movements of the hindlimb (and their timing in relation to movements of the trunk) during terrestrial locomotion in a non-specialized salamander, *Dicamptodon tenebrosus*, and to compare the kinematic patterns with those of other tetrapod taxa. Some basic observations of speed effects on salamander locomotion are also made. The primary focus of this paper is descriptive; a rigorous statistical analysis of speed effects is presented elsewhere (Ashley-Ross, 1994). Some of this material has appeared previously in abstract form (Ashley-Ross, 1990).

Materials and methods

Animals

The Pacific giant salamander (*Dicamptodon tenebrosus* Good, 1989) was chosen as the subject for this study as this species leads a generalized terrestrial existence after metamorphosis, with no specializations for burrowing. In addition, *Dicamptodon* demonstrates good walking ability and has robust limbs. Five individuals collected as

larvae in Mendocino County, CA (California scientific collector permits no. 7058 and no. 7614), were used for this study. At the time of these recordings, all had recently (within 3 months) and completely metamorphosed. Specimens were anaesthetized with MS-222 and their snout–vent lengths (SVL; measured from the tip of the snout to the anterior angle of the vent) were measured with calipers. In addition, the position of the acetabulum was determined by palpation of the hip region, and the distance that the acetabulum lay cranially of the ilium on the left side was also measured with calipers (see description of variables, below). The SVLs of the specimens used were as follows: animal 1, 9.51 cm; animal 2, 9.62 cm; animal 3, 8.14 cm; animal 4, 8.51 cm; animal 5, 8.09 cm.

Video recording

Salamanders were videotaped walking on a variable-speed, motor-driven treadmill. White dots were painted (using Testor's flat white model paint) over the dorsal ends of the two ilia, at the left knee, at the distal end of the left fibula and in a series of 7–9 dots along the animal's midline (points were equally spaced, beginning at a point between the two scapulae and ending between the two ilia) to ensure reliable identification of these points. Dissection of a preserved specimen revealed that *Dicamptodon* have 13 vertebrae (inclusive) between the pectoral and pelvic girdles; therefore, adjacent midline marker dots spanned 1–2 intervertebral joints.

Salamanders walked readily towards a 'hiding place', a section of black polyvinylchloride tubing suspended at the far end of the treadmill, or were encouraged to walk by touching or gently squeezing the base of the tail. Animals were always placed on the treadmill so that their left side faced the cameras. Salamanders were videotaped using a NAC high-speed video system (NAC Industries, Japan; sampling frequency 200 fields s⁻¹) equipped with two cameras: one for a direct lateral view, and the other, which was equipped with a zoom lens, for a dorsal view through a front-surface mirror inclined above the treadmill surface at an angle of 45°. The zoom lens was adjusted so that both lateral and dorsal views of a scale bar were the same size. A 1 cm grid was affixed to the rear wall of the treadmill, below the mirror, and the treadmill belt was marked with lines 10 cm apart to enable accurate distance measurements to be taken from the videotape frames.

Video analysis

Only stride sequences that showed the animal in continuous, steady-speed motion were selected for analysis. Strides in which locomotion started or stopped were not used. Gaits were classified following the conventions of Hildebrand (1976). Three strides were obtained for each animal at both a moderate diagonal-couplets lateral sequence walk (see Results; average speed 0.77 SVL s⁻¹; referred to as the 'walk' hereafter) and a trot (average speed 2.90 SVL s⁻¹; referred to as the 'trot' hereafter). At least 20 equally spaced fields from each stride were captured on magnetic or optical media for later digitizing. A video-analysis program (MeasurementTV, DataCrunch Software, San Clemente, CA) was used to digitize the coordinates of the painted marker points. All marker points were digitized from the dorsal view, while only the points over the left ilium, knee and ankle were also digitized from the lateral view. These coordinates were

imported into a spreadsheet program, which was used to compute the angle variables defined below. The curves produced by plotting these angles over the duration of a stride (the 'kinematic profile') were smoothed by Gaussian filtering using the curve-fitting and analysis program Igor (WaveMetrics, Lake Oswego, OR) in order to reduce digitizing error. These smoothed kinematic profiles were then used for determination of minimum and maximum values for each kinematic variable (defined below).

Definition of variables

A *stride* was defined as the time (in ms) from left hindfoot contact with the treadmill belt to the subsequent left hindfoot contact. *Cycle duration* was the time between the start of one stride and the start of the following stride. *Pelvic girdle angle* was defined as the angle between the line connecting the two marker points over the ilia ('pelvic girdle line') and the edge of the treadmill (Fig. 1A). *Pelvic girdle–femur angle* was measured between the pelvic girdle line and the line connecting the calculated position of the acetabulum (see Animals, above) and the knee marker dot ('femur line'; Fig. 1B). This angle was zero when the femur was in line with the pelvic girdle line, and assumed positive values when the femur was inclined forward of that line (protracted), and negative values when inclined back of that line (retracted). *Femur–crus angle* was measured between the femur line and the line connecting the knee marker and the dot at the distal end of the fibula ('crus line'; Fig. 1C). Two different types of variables measured lateral bending of the trunk. A measure of the overall bending of the trunk was provided by the angle between the lines connecting the anteriormost and posteriormost pairs of marker dots in the trunk region (*anterior–posterior angle*; Fig. 1D). Localized bending in the anterior, middle and posterior regions of the trunk was measured by the angle between adjacent pairs of midline markers in the appropriate trunk regions (*trunk segment angle*, Fig. 1E). All of the preceding angle variables were calculated from coordinates digitized in the dorsal view of the salamander. One additional angle variable, the *lateral crus angle*, was digitized from the lateral view of the animal and was measured as the angle between the line connecting the knee and fibula marker points and the treadmill surface (Fig. 1F).

Several timing variables were also measured. *Contact interval* (footfall to lifting of the foot), relative timing between the beginning of stance and the maximum value of several variables (pelvic girdle angle, pelvic girdle–femur angle) and relative timing between the beginning of swing and the minimum value of several variables (pelvic girdle angle, pelvic girdle–femur angle, femur–crus angle) were all expressed as a percentage of the step cycle duration. Hildebrand-style footfall diagrams (Hildebrand, 1966, 1976) were also generated by plotting foot contact intervals as a percentage of the step cycle.

Results

Dicamptodon typically use a diagonal-couplets lateral sequence walk (in which the hind footfall is followed by that of the forefoot on the same side of the body, and the footfalls of a diagonal limb pair are closely spaced in time; Hildebrand, 1976) or a trot (in which diagonal limb pairs move more or less in synchrony; Hildebrand, 1976), though there is variation from stride to stride within individuals. The most common variation

observed was that in a diagonal pair of limbs, the order in which footfalls occurred was reversed from that expected. For instance, the expected order during a lateral sequence walk for the left forefoot/right hindfoot diagonal pair is LF up, RH up, LF down, RH down. In 30% of strides analyzed, such an order was modified to be LF up, RH up, RH down, LF down. In 11% of strides, the feet of a diagonal pair lifted off or struck the ground synchronously. Diagonal gaits (in which the strike of a hindfoot was followed by that of the forefoot on the opposite side of the body) were never observed. A

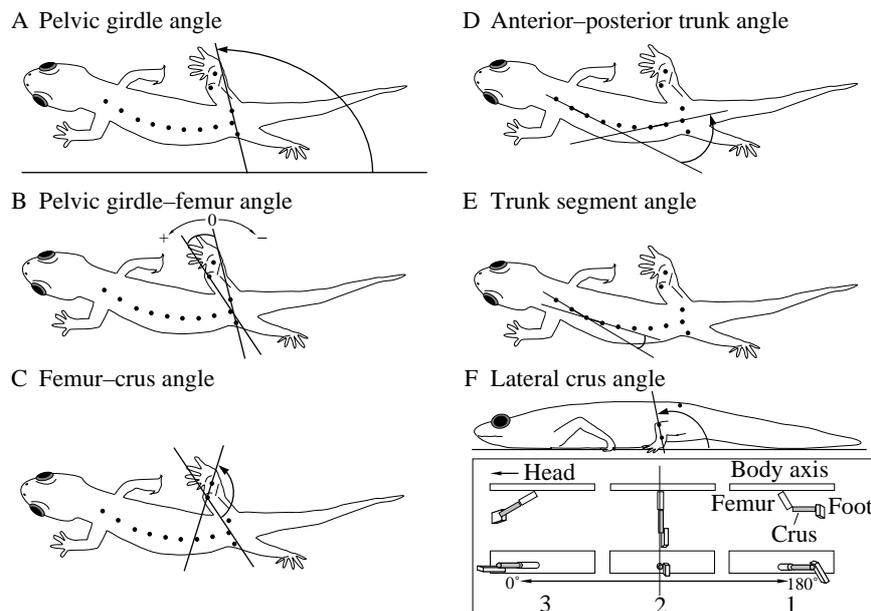


Fig. 1. Schematic representation of the angular variables measured. (A) Pelvic girdle angle in degrees. (B) Pelvic girdle–femur angle. The angle is 0° when the femur is in line with the two ilia, positive when the femur is protracted relative to that position, and negative when it is retracted relative to that position. (C) Femur–crurus angle. (D) Anterior–posterior trunk angle. (E) Trunk segment angle. Anterior trunk segment is illustrated. (F) Lateral crus angle. The salamander outline was traced from a video frame. See text for details. In the dorsal view illustrated, the marker dots accurately represent the location of the markers on the back of the salamander, which have been painted along the midline of the animal. They appear to be off the midline for two reasons: (i) the vertebral column undergoes torsion during stepping movements, and (ii) the belly of the salamander tends to bulge out towards the concave side of the trunk. See Fig. 2 for more examples of these phenomena. Inset: schematic diagram to illustrate the abrupt switch of lateral crus angle from 180° to 0° as the leg is swung forwards in the ‘overarm crawl’ during protraction. Upper panels illustrate the left hindlimb (femur, crus and foot) and adjacent regions of the axial skeleton from the dorsal view, lower panels show the lateral view. The inset model is in the same orientation as the other figure panels (the salamander would be facing to the left). The stippled region represents the crus. Panel 1: the limb is fully retracted, and the crus is parallel to the treadmill surface (lateral crus angle 180°). Panel 2: the limb is midway through protraction and is sticking straight out towards the camera in the lateral view. The thin line follows the long axis of the crus in this position and represents the plane at which the 180° -to- 0° switch occurs. Panel 3: the limb is protracted, with the crus parallel to the treadmill surface (lateral crus angle 0°).

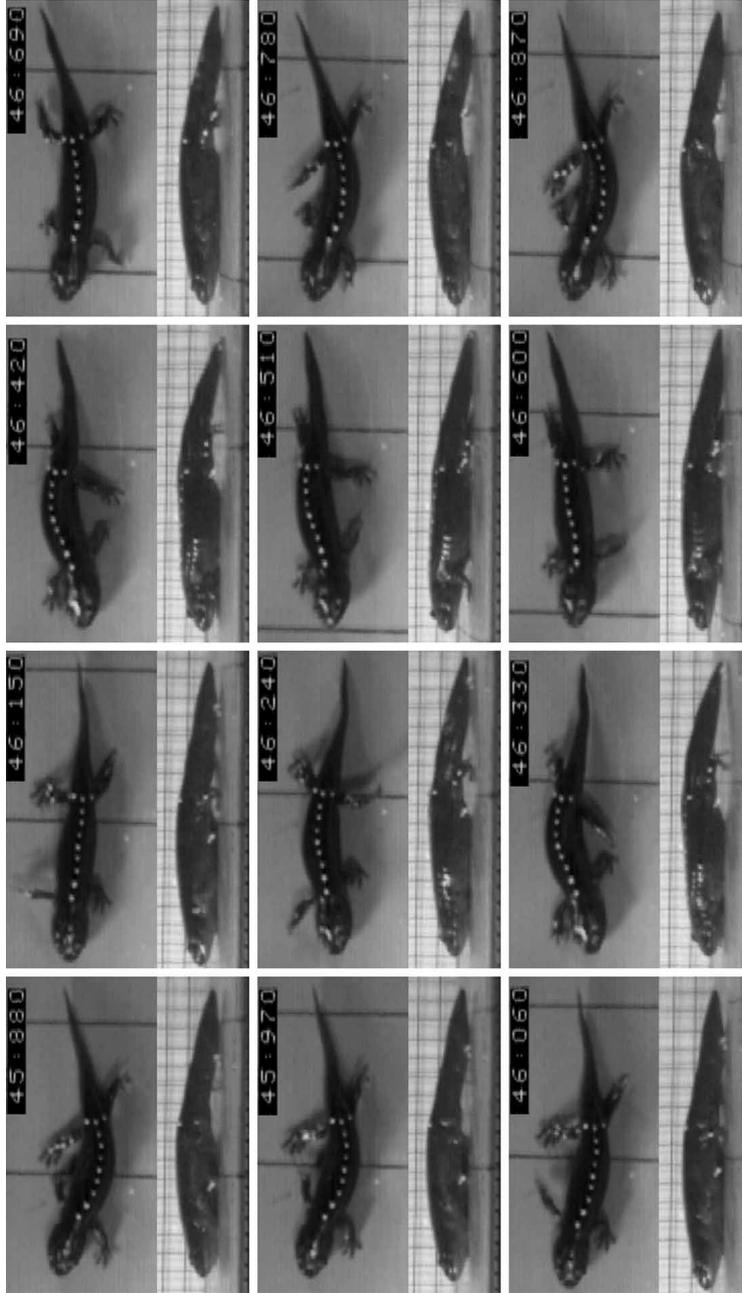


Fig. 2. Sequence of frames taken from the high-speed video showing one complete stride (lasting 990 ms) of *Dicamptodon tenebrosus* at a walk (0.8 SVL s^{-1}). The sequence progresses down columns. Frames are equally spaced in time. Frames from the original video tape were cropped and composited using Adobe Photoshop (Adobe Systems Inc., Mountain View, CA). Note that the dorsal view (upper panel of each frame) is filmed through a 45° mirror, so that the marked left leg is towards the top of each frame. Also note the relatively small percentage of time spent in the swing phase of the stride.

representative (lateral sequence) stride at a walking pace of 0.8 SVL s^{-1} is shown in Fig. 2. Note that the majority of the cycle duration is taken up by the stance phase, and that the swing phase is confined to approximately 25 % of the time taken by a stride at this speed. Note also that, even at a walking pace, there are substantial periods during the stride when the animal is supported solely by a diagonal pair of limbs (Figs 2, 3A). This pattern is accentuated as the animal's speed increases and the gait converges on a trot (Fig. 3B). The average gait diagram in Fig. 3A is classified in Hildebrand's (1976) gait formula scheme as a slow diagonal-couplets lateral-sequence walk. The left hindlimb spends 72 % of the step cycle on the ground, while the strike of the left forefoot follows the strike of the left hindfoot by 43 % of the stride. The higher-speed gait shown in Fig. 3B is classified as a fast trot, with the left hindlimb spending 53 % of the step cycle on the ground, and the left forefoot following the left hindfoot by 50 % of the stride. In both the walk and trot, most of the time during the stride is spent with the animal supported by either two legs (40.6 % walk, 91.5 % trot) or four legs (34.8 % walk, 4.8 % trot), with a shorter transition time between these two states when the animal is supported by three legs (24.6 % walk, 3.7 % trot).

Fig. 4 shows representative kinematic profiles of the major angular variables measured for three walking strides from one salamander. As the stride begins with the placement of the left foot on the treadmill, the pelvic girdle is oriented with the left ilium forwards (Fig. 4A; also refer to Fig. 2), the femur is angled forward relative to the pelvic girdle

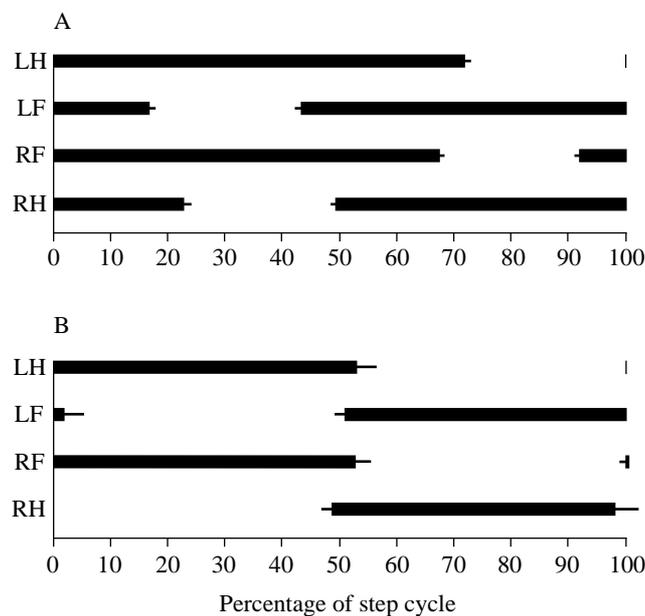


Fig. 3. Hildebrand-style gait diagrams for *Dicamptodon tenebrosus* (A) walking and (B) running versus percentage of the step cycle. Thick bars represent the time when the foot is in contact with the ground; the ends of the bars are calculated as the mean touchdown/lift-off times for all individuals. Thin bars represent one standard error of the mean, $N=20$ for A, $N=16$ for B. LH, left hindfoot; LF, left forefoot; RF, right forefoot; RH, right hindfoot.

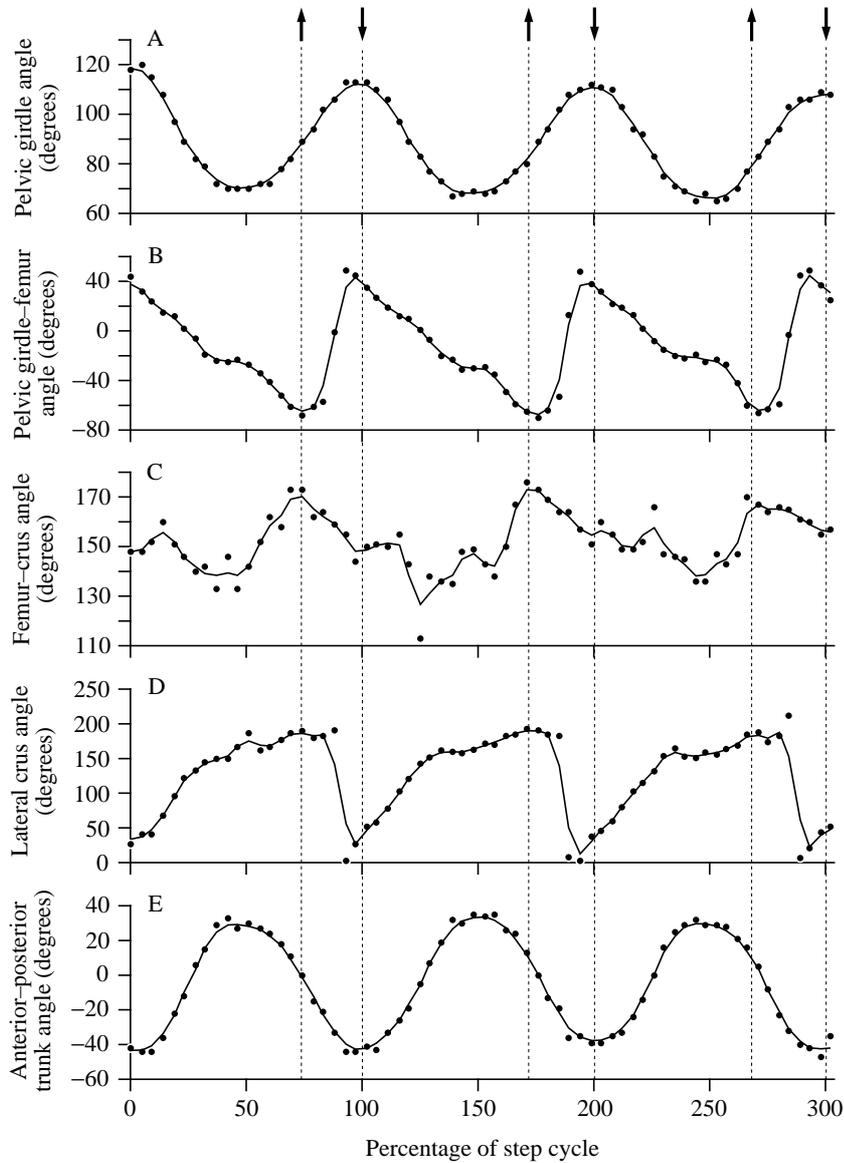


Fig. 4. Representative kinematic profiles of five angle variables defined in Fig. 1 from three strides of *Dicamptodon tenebrosus 2* versus percentage of the step cycle. All angles are measured in degrees. (A) Pelvic girdle angle. (B) Pelvic girdle-femur angle. (C) Femur-crurus angle. (D) Lateral crus angle. (E) Anterior-posterior trunk angle. Negative angles indicate that the trunk is concave to the left. In all panels, dots are raw data and lines are the smoothed kinematic profiles used to calculate variable minima and maxima (see Materials and methods: video analysis). Dotted lines with upward-pointing arrows indicate the time of the beginning of the swing phase; dotted lines with downward-pointing arrows indicate placement of the left hindfoot for the beginning of the next stride.

(Fig. 4B) and the crus is extended, making a shallow angle with the treadmill surface (Fig. 4C,D). At this point, the trunk is concave towards the left (Fig. 4E). As the stride progresses, one sees straightening of the trunk (towards 0° ; Fig. 4E) followed by flexion towards the opposite side and smooth oscillation of the pelvic girdle. The knee joint (Fig. 4C) shows the most variable kinematic profile of this sequence, but is generally characterized by slight extension (or is unchanged) during the early stance phase until the contralateral hindlimb begins its swing phase, followed by flexion as the salamander pulls its body towards the foot, followed by extension as the hip joint passes over the foot and the animal begins to push off with the foot. The knee joint reaches its greatest extension at the time of foot lift-off, after which it flexes throughout the swing phase. The femur is retracted steadily until the opposite hindfoot is placed on the ground, which coincides with the time when the knee joint begins to extend. At this point, the femur decreases its rate of retraction for a short time, followed by resumption of a more rapid rate of retraction. During the swing phase, the pelvic girdle–femur angle shows a rapid increase (from negative to positive values) and the lateral crus angle drops abruptly to zero as the entire leg is protracted by being swung straight out to the side of the animal in an ‘overarm crawl’ motion (similar to that used in swimming in humans). The abrupt switch from 180° to 0° in the lateral crus angle is an unavoidable result of the manner in which the angle is calculated (see inset to Fig. 1F); when the ankle marker is straight out to the right of the knee marker (on the video screen), the angle is 180° (Fig. 1F, inset panel 1), but when the leg is protracted, it is swung in a horizontal arc so that the crus comes to point directly at the camera (inset panel 2), and then continues on so that the ankle marker is straight out to the left of the knee marker (inset panel 3). The calculated angle is then 0° and, consequently, the lateral crus angle will switch almost instantaneously from 180° to 0° .

Table 1 summarizes the mean values for the kinematic variables measured for both a walk and a trot (also refer to Fig. 4 for representative kinematic profiles). Mean stride length at a walk (mean speed 0.77 SVL s^{-1}) was 72.9 % of SVL, increasing to over 100 % of SVL at a trot (mean speed 2.90 SVL s^{-1}). Both the cycle duration (0.97 s walk, 0.42 s trot) and the contact interval (72 % walk, 53 % trot; see also Fig. 3) decreased in the transition from a walk to a trot. The pelvic girdle and the trunk oscillate symmetrically through ranges of 38.5° and 65.7° , respectively, at a walk. Both of these oscillations increase their amplitudes at a trot (to 73.3° and 88.1° respectively). At a walking pace, the pelvic girdle reaches its minimum value 22 % of the cycle before the swing phase begins, resulting in the pelvic girdle having returned nearly half way to its starting position by the time the foot is lifted from the ground. Maximum pelvic girdle angle occurs almost simultaneously with the beginning of the stride. In contrast, during trotting the minimum pelvic girdle angle is reached only 10 % of the step cycle before the beginning of swing, while the maximum value is reached approximately 7 % before the beginning of the next stride. The pelvic girdle–femur angle during walking moves through a range of 106° as it protracts from a minimum angle of -55° just before the beginning of the swing phase to a maximum of 51° slightly before the foot is put down for the beginning of the next stride. The femur is maximally retracted just before the start of the swing phase and attains maximal protraction just before the beginning of the next stride. Femoral excursion is essentially unchanged in trotting, with the exception that

maximal retraction is reached after the foot has been lifted from the ground. The femur–crus angle has a range of approximately 65° , beginning with the knee nearly straight at 173° during walking, and flexing to 108° . Knee flexion is greatest 43% of the step cycle before the beginning of swing phase. In trotting, the excursion of the knee joint is unchanged except that the minimum femur–crus angle is reached just 8% of the cycle before the initiation of swing phase. From the lateral view, the crus is angled to the treadmill surface at an average of 42° and reaches a maximum of 185° before the foot is lifted at a walk (indicating that the ankle is higher than the knee, which occurs when the foot rolls up on the toes during late stance phase). These values are unchanged in trotting.

Fig. 5 illustrates the lateral displacements, measured from the dorsal view, of the marker points at the left ilium, knee and ankle for the same strides shown in Fig. 4. The ankle remains relatively fixed throughout the stance phase. At the beginning of the swing phase, the ankle shows an increase in lateral displacement as the limb is swung straight out from the body during protraction. The foot is brought far forwards, with the trunk flexed concave towards the left side, resulting in the sharp decrease in ankle displacement, and finally moves back laterally before foot touchdown. In the early part of the stride, the knee and ilium show decreases in lateral displacement. The knee marker

Table 1. Summary of kinematic values measured from *Dicamptodon tenebrosus* walking and trotting

Variable	Walk	Trot
Stride length (% SVL)	72.9 (5.47)	107.1 (24.68)
Cycle duration (s)	0.97 (0.11)	0.42 (0.14)
Contact interval (% of step cycle)	72.0 (5.42)	52.9 (13.47)
Pelvic girdle angle range (degrees)	38.5 (6.97)	73.3 (29.06)
Minimum pelvic girdle–femur angle (degrees)	–55.2 (19.79)	–49.1 (14.28)
Maximum pelvic girdle–femur angle (degrees)	51.1 (8.74)	57.9 (8.65)
Pelvic girdle–femur angle range (degrees)	106.2 (13.54)	106.9 (14.40)
Minimum femur–crus angle (degrees)	108.0 (17.67)	102.3 (17.34)
Maximum femur–crus angle (degrees)	172.6 (19.59)	159.2 (14.12)
Femur–crus angle range (degrees)	64.7 (20.96)	56.9 (14.14)
Maximum lateral crus angle (degrees)	185.0 (7.32)	192.2 (8.18)
Initial crus angle (degrees)	42.0 (15.74)	52.6 (26.47)
Anterior–posterior trunk angle range (degrees)	65.7 (13.95)	88.1 (12.26)
Minimum pelvic girdle angle/swing initiation phase (% of step cycle)	–22.2 (6.28)	–9.8 (12.14)
Maximum pelvic girdle angle/stance initiation phase (% of step cycle)	0.2 (3.88)	–7.0 (7.89)
Minimum pelvic girdle–femur angle/swing initiation phase (% of step cycle)	–1.6 (5.51)	10.2 (12.00)
Maximum pelvic girdle–femur angle/stance initiation phase (% of step cycle)	–3.3 (3.52)	–6.8 (4.71)
Minimum femur–crus angle/swing initiation phase (% of step cycle)	–42.8 (7.73)	–8.2 (36.62)

All values are given as mean (standard deviation) and are calculated from three strides for each of five individuals ($N=15$ for each entry).

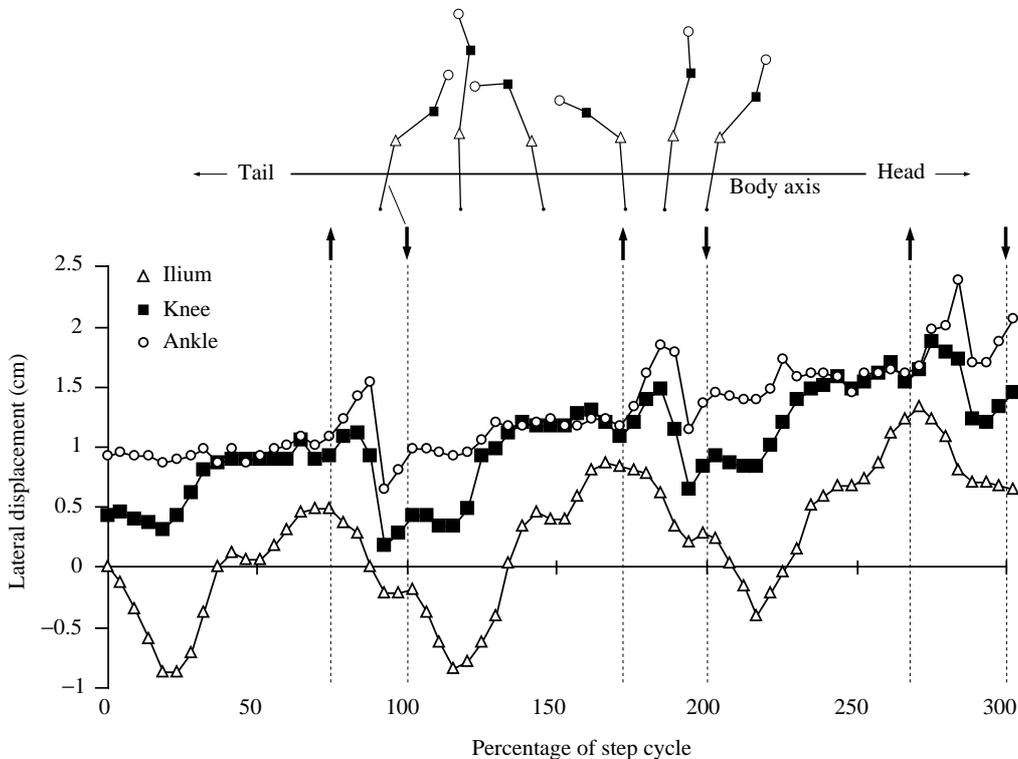


Fig. 5. Plots of lateral displacement, from the dorsal view, of painted marker points over the left ilium, the left knee and the left ankle *versus* percentage of the step cycle for the three strides shown in Fig. 4. Dotted lines with upward-pointing arrows indicate the time of the beginning of the swing phase; dotted lines with downward-pointing arrows indicate placement of the left hindfoot for the beginning of the next stride. Stick figures above the middle stride represent the pelvic girdle line, the femur line and the crus line, and indicate the position of the pelvic girdle and limb at the indicated times. The animal would be moving from left to right on the graph.

records a relatively small movement towards the body as the crus pivots about the fixed ankle. The ilium marker shows a larger-amplitude movement towards the contralateral limb as it is influenced by the double movement of the crus pivoting about the ankle and the femur pivoting about the knee joint, which is extending slightly (Fig. 4C). This movement towards the contralateral side continues until the contralateral hindlimb is lifted, at which point the pelvic girdle begins to move back towards the supporting side, and the knee joint flexes, pulling the knee marker towards the ankle. The knee is positioned directly ahead of the ankle as the knee joint begins to extend (Figs 4C, 5), and the ilium moves further towards the supporting foot. As the foot is lifted, the ilium moves back towards the contralateral (supporting) side, and the knee marker shows a displacement increase and decrease paralleling that of the ankle marker as the leg is protracted.

To visualize better how the salamander as a whole is moving throughout a stride, Fig. 6

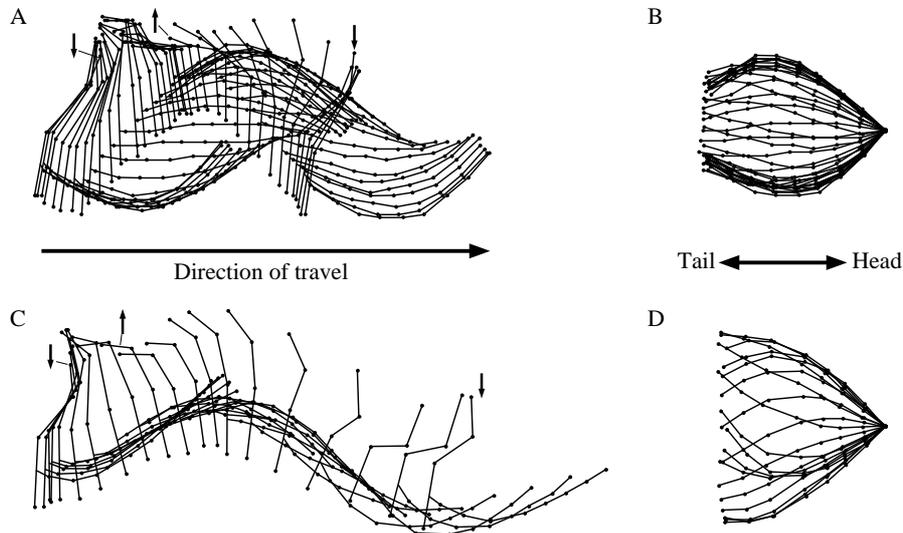


Fig. 6. Stick figure plots from the dorsal view of trunk and left limb positions throughout a complete stride for a walk (A,B) and a trot (C,D). The stick figures were made by connecting the marker points over the midline, pelvic girdle (both right and left ilia) and left hindlimb (knee and ankle). A and C show the spatial progression of the animal through the stride. The salamander is moving from left to right (the head is towards the right). The downward-pointing arrows indicate the time of placement of the foot at the beginning and end of the stride, the upward-pointing arrow indicates the lifting of the foot. In B and D, all the trunk sections of the stick figures from the corresponding sequence have been superimposed by lining them up on the anteriormost midline marker dot. (A,B) *D. tenebrosus* 4, (C,D) *D. tenebrosus* 3. These strides were chosen because they are particularly clear examples of standing wave and travelling wave patterns. Other strides from these and other individuals were similar in appearance, but tended to show more blending of standing and travelling wave characteristics.

shows stick figures made by connecting the marker dots along the midline, the two ilia and over the left knee and ankle for representative strides at a walk (Fig. 6A) and a trot (Fig. 6C). As the stride progresses, the entire animal swings forward on the fixed pivot point of the foot, then the body is pulled over towards the foot as the knee flexes, the body is pushed forward on the foot as the knee joint extends and the limb is further retracted, and finally the body weight is shifted back towards the contralateral side during the swing phase. At both walking and trotting paces, the limb has begun its retraction phase before the foot is placed on the ground for the beginning of the next stride (Fig. 6A,C). Movements of the trunk region may contribute to the effective stride length. As can be seen from Fig. 6A, at a walking pace the salamander spends the early part of the stride with the trunk stably flexed with concave towards the left, followed by a smooth transition through a straightened position to being flexed with concave to the right once the right leg enters its swing phase and coinciding with the left knee moving past the point where it is ahead of the left ankle. The trunk has already begun to be flexed back to its original position before the foot is lifted, and it completes this movement during the

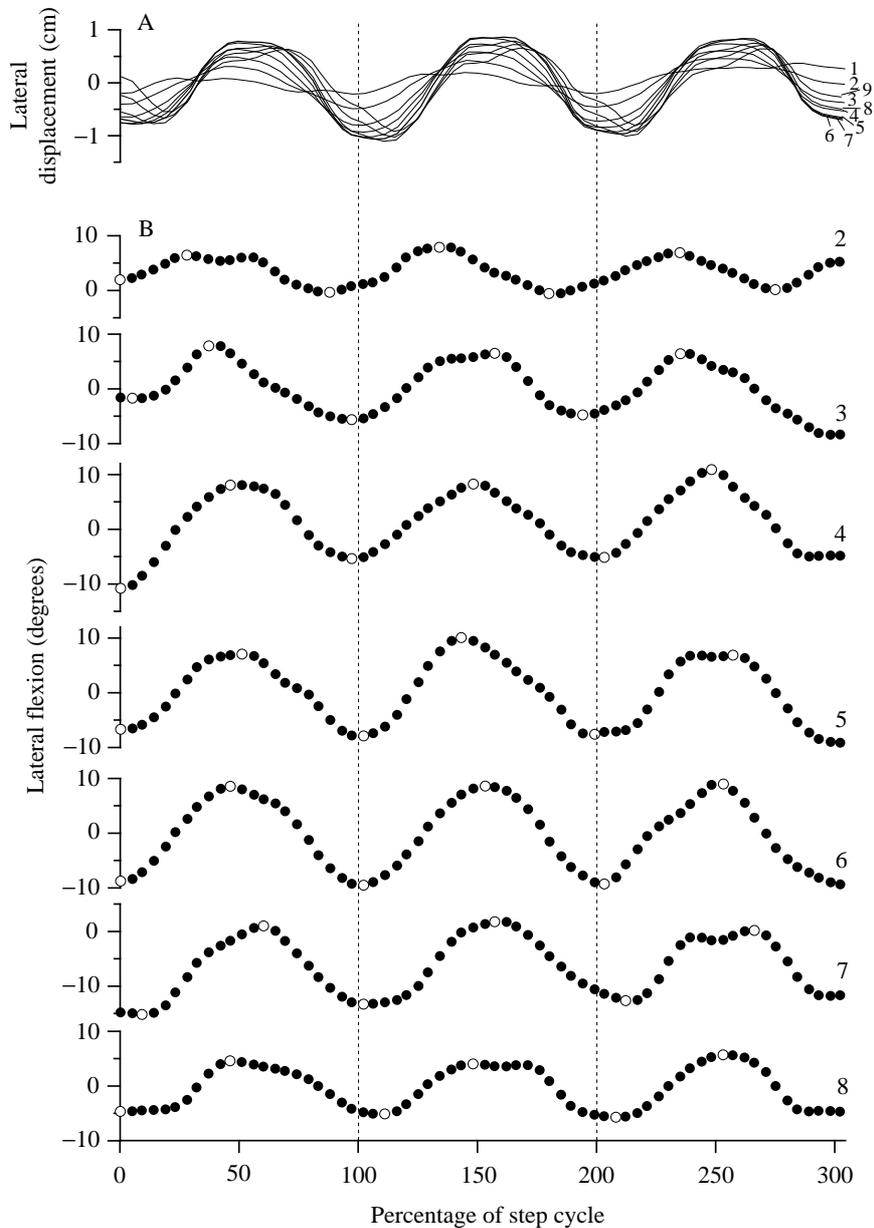


Fig. 7. (A) Superimposed traces of lateral displacement of the nine midline marker dots *versus* percentage of the step cycle for three strides at a walking pace of *Dicamptodon tenebrosus* 4. Marker 1 is the anteriormost point; marker 9 is the posteriormost dot. Zero displacement is arbitrary. (B) Lateral flexion at the numbered midline marker points. Each numbered point is the vertex of the angle being measured; for instance, flexion measured at marker 2 is the angle between the line segment joining markers 1 and 2 and the line segment joining markers 2 and 3. Open dots indicate minimum and maximum flexion for each stride.

swing phase of the left leg. Note that the trunk movements describe an alternation between two stable curved configurations; the transition between one curve and the other serves to advance the trunk by one 'half-wavelength'. This pattern tends to conform to that usually described for a standing wave with nodes in the pectoral and pelvic girdle regions, which can be seen more clearly when the various stick figures for the axial markers are superimposed (Fig. 6B).

In contrast to this pattern for the walking pace, *Dicamptodon* shows more travelling-wave characteristics when trotting. As shown in Fig. 6C, all points on the trunk pass along approximately the same path, which is usually indicative of a travelling wave passing down the trunk. That the trunk does not follow a simple side-to-side bending pattern can be seen particularly well in the superimposed stick figure (Fig. 6D).

Fig. 7 shows the lateral displacement (Fig. 7A) and lateral flexion (Fig. 7B) experienced at each of the trunk marker points for three strides at a walking pace. As expected for a primarily standing wave pattern, displacement is greatest in amplitude towards the middle of the trunk and least at the anterior and posterior regions (Fig. 7A, Table 2). Flexion is also greatest in amplitude in the middle regions of the trunk, and maximal flexion is nearly synchronous at all segments (Fig. 7B).

Fig. 8 plots lateral displacement and flexion for two strides at a trot. Though the displacement patterns are not symmetrical for the two strides, the first stride in particular shows that a wave of maximal displacement passes posteriorly down the trunk (Fig. 8A), as would be expected of a travelling wave pattern. However, a similar travelling wave of maximal flexion does not seem to be present (Fig. 8B). Instead, maximal flexion seems to be nearly synchronous at all trunk levels, with the only segmental difference being that the degree of flexion (and displacement) is greater at the middle and posterior trunk regions than at the anterior segments (Fig. 8B, Table 2). Overall trunk flexion is greater during trotting than during walking (Table 1).

Discussion

Gaits

The sprawling posture has been considered to be intrinsically unstable and inefficient owing to the inability to balance the centre of gravity over the legs. It has been argued that animals that sprawl would need to choose extremely stable gaits, offering a broad base of support to avoid pitching over, particularly at low speeds (Hildebrand, 1966, 1985; Gray, 1968; Edwards, 1977). The lateral sequence walk has been described as theoretically the most stable gait because the centre of gravity is always located inside a triangle formed by the three supporting legs (Hildebrand, 1985). *Dicamptodon* does use the lateral sequence walk; however, at a walk there is relatively little time during the stride when the animal is supported by three legs. The largest proportion of the stride is spent supported by diagonal limb pairs (40.6%), followed by periods of support by four legs (34.8%). Periods of support by three legs occupied the smallest fraction of the stride (24.6%). During a trot, the percentage of support by two legs increases to 91.5%, with only 4.8% of the cycle supported by four legs and only 3.7% supported by three.

In this study, the fastest sustainable gait observed in *Dicamptodon* was a trot. However,

Table 2. Amplitudes of lateral displacements and flexion angles measured at midline marker points of *Dicamptodon* 1, 2 and 4, each of which was marked with nine midline dots

	Marker								
	1	2	3	4	5	6	7	8	9
Speed									
Walk									
Displacement (cm)	0.71 (0.30)	1.13 (0.26)	1.56 (0.32)	1.92 (0.41)	2.14 (0.46)	2.20 (0.49)	2.13 (0.49)	1.92 (0.46)	1.64 (0.44)
Flexion (degrees)	15.19 (1.74)	19.13 (3.72)	22.63 (4.59)	24.11 (4.21)	24.76 (5.60)	23.01 (6.26)	21.58 (7.17)		
Trot									
Displacement (cm)	1.73 (0.93)	1.69 (0.95)	1.86 (0.89)	2.14 (0.90)	2.33 (0.91)	2.44 (0.94)	2.43 (0.94)	2.32 (0.95)	2.20 (0.88)
Flexion (degrees)	18.72 (3.62)	21.18 (5.06)	23.53 (5.01)	24.80 (3.36)	27.15 (4.73)	28.25 (3.88)	27.49 (4.12)		

All values are given as mean (standard deviation) and are calculated from three strides for each of three individuals (total $N=9$ for each entry).

a few sequences were recorded in which the salamander used a symmetrical run with periods of support by a single leg and brief periods of suspension. Speeds for these sequences were approximately 7 SVL s^{-1} . During these strides, there was considerable rocking of the trunk from side to side, as has been described by Snyder (1949) for bipedally running lizards. However, these speeds were not sustainable for more than one or two strides before the salamander landed in an uncoordinated fashion on its belly. At no time was any animal observed to fold the limbs back against the body and progress

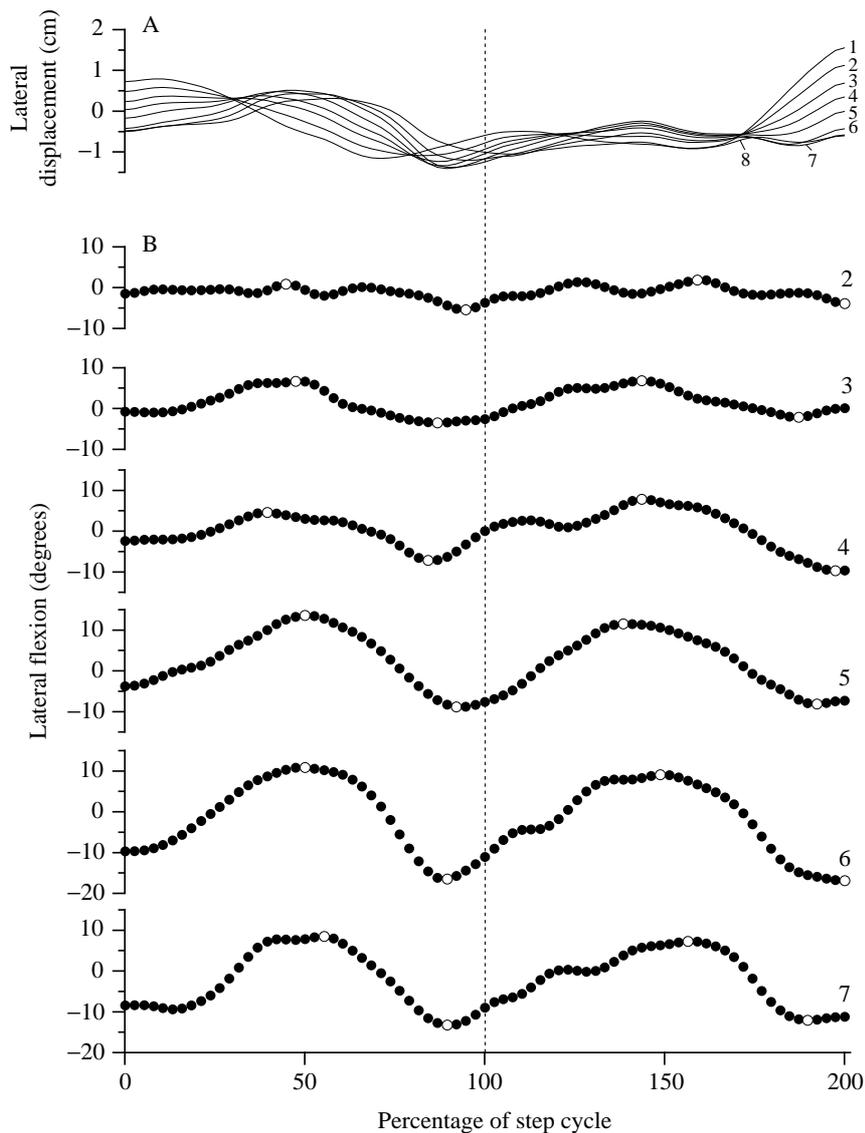


Fig. 8. Lateral displacement (A) and lateral flexion (B) of the nine midline marker dots *versus* percentage of the step cycle for two strides at a running pace for *D. tenebrosus* 3. Same conventions as Fig. 7.

forwards using axial undulation alone, as had been described in the salamander species studied by Edwards (1977).

Salamander limb kinematics

The movements of the various limb segments and their integration with the simultaneous movements of the trunk are complicated (Figs 4, 5, 6). Combining the information in Figs 4 and 5 yields some interesting observations. First, the body axis is not maintained in a position midway between the feet throughout the stride. There is considerable movement from side to side by the body in the region of the pelvic girdle, as shown by the trace for the ilium in Fig. 5. It is reasonable to assume that the same kinds of movements are also taking place at the pectoral girdle (with reduced amplitude; see Table 2) as the forelimbs progress through their step cycle. Since the diagonal limbs are roughly synchronized in their movements, one would expect to see the same displacements (in the opposite direction) of the pectoral girdle taking place at the contralateral forelimb. The greatest displacement towards the left hindlimb by the pelvic girdle occurs just before the left hindfoot leaves the ground, so one would expect to see the greatest displacement of the pectoral girdle towards the right forelimb at approximately the same time. These simultaneous movements would result in the vertebral column assuming an **S** shape. Note that such a pattern can be seen in Fig. 2 (panel 46:420), and that **S**-shaped configurations are present in the stick figure overlays shown in Fig. 6B,D.

Second, in spite of these **S**-shaped curves and the consequent disruption of a pure standing wave pattern, the pattern of oscillation of the pelvic girdle and the anterior–posterior trunk angle remain remarkably smooth (Fig. 4A,E). Note that these variables have progressed approximately half way back towards their initial values before the foot is lifted from the ground. Thus, at a walking pace, the salamander is not maximizing stride length, since the full arcs travelled by the pelvic girdle and trunk segments are not contributing to the effective limb length (Fig. 9). As speed increases, the swing phase begins earlier in the step cycle and occupies a larger proportion of the step cycle. The swing phase begins closer to the time when the pelvic girdle begins its oscillation back to its initial position. Thus, the oscillation of the pelvic girdle is able to contribute more to the effective limb length, and consequent stride length, at higher speeds (Fig. 9). However, seeming to undermine this effect is the tendency for maximum femoral retraction to occur after the beginning of swing phase and for maximum knee flexion to occur closer to the beginning of swing (reducing the time available for knee extension in late stance) during trotting (Table 1).

Third, the ‘double crank’ system described by Barclay (1946; explained in Fig. 10A) for translating rotation of the humerus to anterior-to-posterior movement of the forefoot in the toad cannot be transplanted wholesale to the analysis of the salamander hindlimb, as has been implied previously (Barclay, 1946; Gray, 1968; Edwards, 1977, 1989; Peters and Goslow, 1983). The double crank model is well suited to the toad forelimb for three reasons: (1) the radio-ulna maintains a relatively constant angle to the humerus during the stance phase; (2) the humerus does not undergo extensive retraction, nor does the elbow joint extend far to push the animal forward (Barclay, 1946; see his Fig. 2) in late stance; and (3) the body does not move very far laterally towards the supporting foot (Fig. 10A).

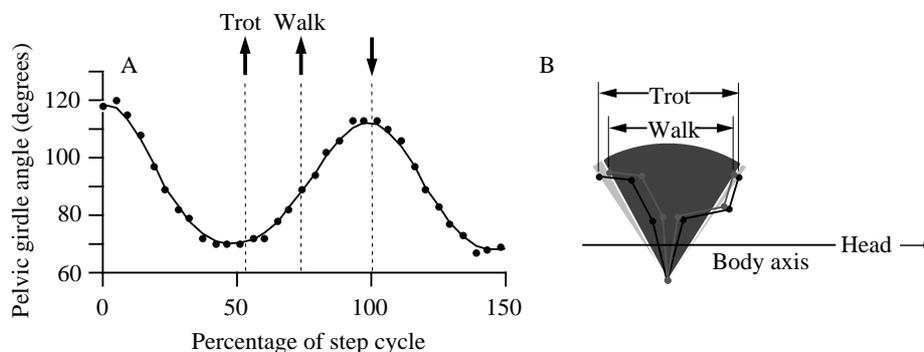


Fig. 9. Effect of minimum pelvic girdle angle/swing initiation phase value on stride length. (A) Pelvic girdle angle oscillation over 1.5 strides. Dotted line with downward-pointing arrow indicates the beginning of the next stride, lines with upward-pointing arrows show the relative phasing of swing initiation at a walk and a trot. Swing during trotting coincides more closely with the minimum pelvic girdle angle. (B) Diagram to show the contribution of pelvic girdle oscillation to distance moved by the leg during the swing. Stick figures (from the dorsal view) represent the pelvic girdle (right and left ilia), left knee and left ankle. See Fig. 6 for comparison. Black stick-figure limb represents the trot, grey stick-figure represents the walk. Joint angles are the same in both, only the excursion of the pelvic girdle is shown differently for the two speeds. The light stippling shows the arc covered by the entire effective limb (from the right ilium to the left ankle) during the swing in the trot, while the dark stippling shows the same arc for the walk. The larger arc made by the pelvic girdle during the swing phase in the trot increases the size of the step.

These three conditions allow the forelimb to act as 'probably the nearest approach to that of a wheel and axle to be found anywhere in the animal kingdom' (Gray, 1968, p. 119). While the double crank system undoubtedly may function for part of the step cycle in the hindlimb of the salamander, it should be recognized that it is able to function for only a short time during the stance phase, in the period between the time when the lateral crus angle has reached 90° (at approximately 25% of the step cycle; Fig. 4D) and the time when the pelvic girdle has moved laterally towards the foot (at approximately 50% of the step cycle; Fig. 5). The reason why it may only function during this short period is that, earlier in the stance, the major axis of the crus lies along roughly the same line as the femur, so that rotation of the femur would result in only a small translation of the ankle (Fig. 10B). Later in the stance, when the femur is strongly retracted with the knee joint extended, rotation of the femur would result in pronation of the foot and might lead to loss of contact with the substratum (Fig. 10B). The data of Peters and Goslow (1983) support these predictions: the activity period of the caudofemoralis muscle (the muscle thought to power the double crank mechanism) does not begin until the knee is fully flexed (and the crus has reached 90°) and stops approximately two-thirds of the way through stance phase.

Fig. 11 schematically summarizes the independent contributions made by each of the angular variables measured from the dorsal view to the overall movement of the salamander. Protraction and retraction of the femur account for most of the movement

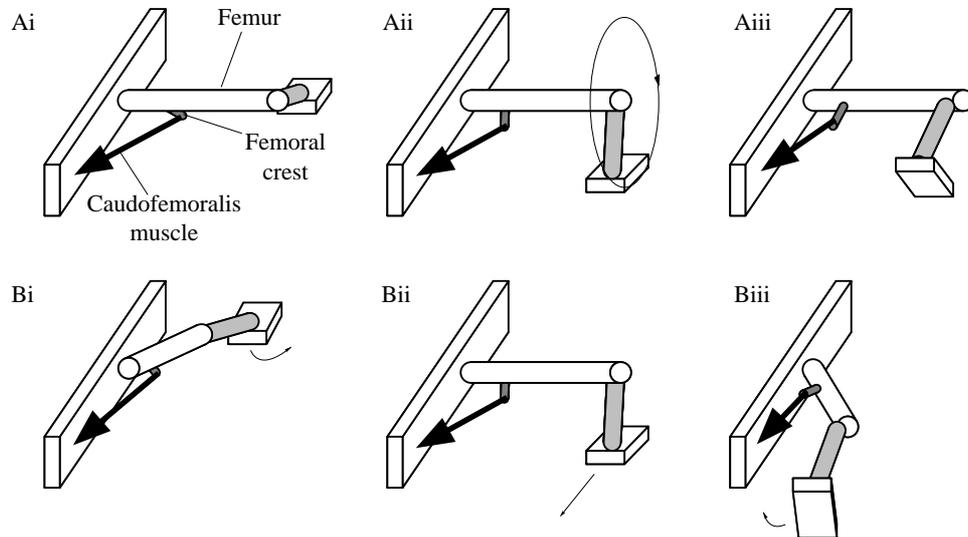


Fig. 10. (A) The double crank mechanism proposed by Barclay (1946) for translating rotation of the humerus or femur into movement of the foot. In the hindlimb, the caudofemoralis muscle (represented by the thick black arrow) originates on the caudal vertebrae and pulls on the femoral crest (Ai), causing the femur to rotate (Aii) and propelling the body over the foot (Aiii). The thin arrow in Aii indicates the trajectory of movement of the foot. Note that this model assumes a relatively constant angle of approximately 90° between the femur and crus throughout the stance phase (modified after Edwards, 1977). (B) A more realistic model of the positions assumed by the leg at the beginning (Bi), middle (Bii) and end (Biii) of the stance phase. Only in Bii is the leg in the appropriate position for the double crank mechanism to operate. At the beginning and end of the stance phase, the probable consequences of femoral rotation are sideways movements of the foot, which would not contribute to effective locomotion.

(and presumably most of the motive power) of the limb, followed by flexion and extension of the knee joint. Back-and-forth oscillations of the pelvic girdle are relatively small, and so would seem to contribute little to any potential increase in stride length. In contrast, bending of the trunk is likely to be an important component for increasing stride length through appropriately timed movements.

Axial undulations

Both standing and travelling wave patterns of axial undulation are used by tetrapods with sprawling posture during locomotion. It has been argued that these two patterns serve different purposes for the animal (Edwards, 1977). Standing waves are thought to act simply to increase the stride length during stepping of the limbs, while travelling waves actively power forward movement. Determination of wave patterns during various types of locomotion yields information on where the primary locomotor power comes from, the axial motor system or the limbs, and on coordination between the two systems.

Swimming salamanders use travelling waves exclusively (Frolich and Biewener, 1992), while both travelling and standing waves have been detected in a number of taxa in

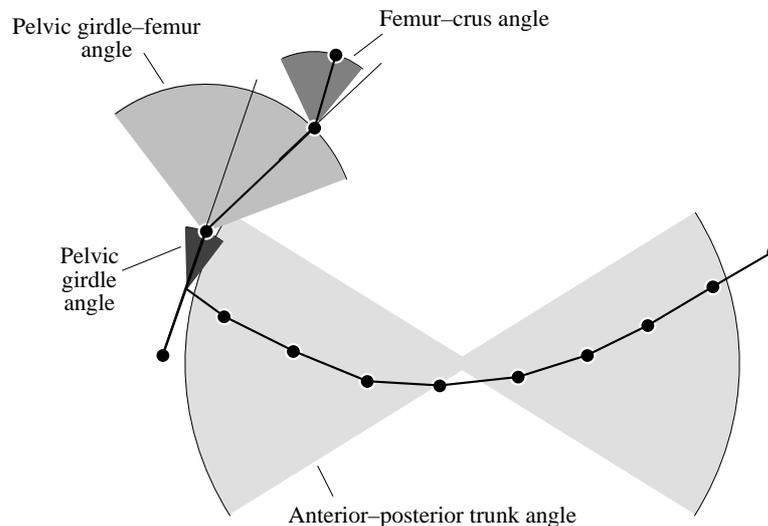


Fig. 11. Schematic diagram of the angular ranges of the variables measured from the dorsal view superimposed on a stick figure. Ranges, minima and maxima are taken from the values given in Table 1. Thin lines are intended as reference lines; the line extending from the pelvic girdle represents a pelvic girdle–femur angle of 0° , while the line extending from the femur line represents a femur–crurus angle of 180° .

terrestrial locomotion. Species with robust limbs typically show a standing wave pattern at slow speeds, which is replaced by travelling waves at higher speeds (Daan and Belterman, 1968; Edwards, 1977; Ritter, 1992). However, Roos (1964) maintained that newts exhibited only standing waves, and only standing waves with nodes at the limb girdles were observed by Frolich and Biewener (1992) in trotting *Ambystoma*. In contrast, Edwards (1977) stated that the salamanders he studied used standing waves at a walking gait and only travelling waves at a trot. One crucial factor seems to be the size and muscularity of the limbs. In both salamanders (Daan and Belterman, 1968) and lizards (Daan and Belterman, 1968; Ritter, 1992), the more reduced are the limbs, the slower the speed at which travelling waves appeared. Lizard species with very diminutive limbs used travelling waves exclusively, even at extremely slow speeds (Daan and Belterman, 1968; Ritter, 1992). In the present study, the pattern of lateral bending at a walking speed most closely matches a standing wave, while at a trot the pattern seems to show features of both standing and travelling waves. Similarly ‘intermediate’ wave patterns, where the amplitude and velocity of the travelling wave is not constant through the trunk, have been shown for lizards by Ritter (1992). Also, the ‘isoskolie’ diagrams of Daan and Belterman (1968) and Edwards (1977) show that the travelling wave patterns of most lizards and salamanders contain elements of standing waves superimposed on them.

One caveat in attempting to determine the role of standing *versus* travelling waves in this study is that markers were located only between the pectoral and pelvic girdles. It may be that the trunk region is too short to resolve accurately waves of bending passing down the body, and marker points down the entire length of the animal would be required

Table 3. Summary of kinematic values reported in the literature for the hindlimbs of various tetrapod taxa

Taxon	Gait	Speed	Stride length	Cycle duration (s)	Contact interval (% of step cycle)	Pelvic girdle rotation (degrees)	Femoral angle (degrees)			Knee joint angle (degrees)			Lateral crus angle (degrees)		Trunk flexion (degrees)	Reference
							Protraction	Retraction	Range	Flexion	Extension	Range	Initial	Maximum		
<i>Dicamptodon</i>	LS walk	0.77 SVL s ⁻¹	0.73 SVL	0.97	72	38.5	51	-55	106	173	65	42	185	66	This study	
	Trot	2.90 SVL s ⁻¹	1.07 SVL	0.42	53	73	58	-49	107	159	57	53	192	88		
	LS walk	0.61 SVL s ⁻¹	-	-	-	27	52	-66	118	134	97	-	-	-		Brinkman (1980b)
<i>Iguana</i>	LS walk	0.61 SVL s ⁻¹	-	-	-	72	31	-68	140-165†	155†	100	138	180†	73	Brinkman (1981) (Figs 1, 2, 3, 5)	
Lizard (<i>Basiliscus</i>)	Trot (bipedal)	-	-	-	-	-	-	-	-	180	105*	85	180	-	Snyder (1949) (Fig. 1)	
Lizard (unidentified)	Trot	-	1 SVL†	-	-	-	-	-	-	166	102*	86	164	-	Snyder (1954) (Fig. 1)	
<i>Varenius</i>	Walk	0.3 km h ⁻¹	0.47-0.54 SVL	1.56-1.66	68-75	-	-	-	-	-	-	-	-	-	Jayne <i>et al.</i> (1990) (Table 1)	
	Walk	0.9 km h ⁻¹	0.66-0.79 SVL	0.78-0.90	61-64	-	-	-	-	-	-	-	-	-	-	
	Walk	1.5 km h ⁻¹	0.75-0.84 SVL	0.57	58-67	-	-	-	-	-	-	-	-	-	-	
<i>Caiman</i>	High walk	0.54-1.35 BL s ⁻¹	-	0.56	57	-	49	-14	63	112	51	108	162	-	Brinkman (1980a) (Figs 1, 2)	
<i>Caiman</i>	LS sprawling walk	-	-	0.77	75	41	48	0	48	132	77	132	180	-	Brinkman (1980a) (Figs 3, 4)	
<i>Alligator</i>	High walk	-	-	-	56	46	38	-18	56	115	63	103	178	-	Schaeffer (1941) (Fig. 17)	
<i>Alligator</i>	High walk	0.1-0.15 m s ⁻¹	-	1.4	73	20-30†	60-70	35-55	15-25†	125-130	80-85	90†	-	20-30†	Gatesy (1991, 1990) (Fig. 3)	
Turtle (<i>Chrysemys</i>)	LS walk	0.34-0.61 CL s ⁻¹	0.66-0.78 SVL	1	74-86†	NA†	63†	0†	63†	98	35†	90†	165-175†	NA†	Walker (1971) (Fig. 5)	
Chick	Walk (bipedal)	-	-	0.35†	52†	NA†	41†	10†	31†	148†	86†	84	154	NA	Johnston and Bekoff (1992)	
Guinea fowl (<i>Numida</i>)	Walk (bipedal)	-	-	1.7	82	NA†	-	-	5*	-	-	50-70†	74	NA	Gatesy (1990) (Fig. 4)	
<i>Monodelphis</i>	LS walk	1.03 BL s ⁻¹	-	-	75	30-40†	-	-	-	-	-	-	-	92	Pridmore (1992) (Fig. 5)	

Table 3. Continued

Taxon	Gait	Speed	Stride length	Cycle duration (s)	Contact interval (% of step cycle)	Pelvic girdle rotation (degrees)	Femoral angle (degrees)			Knee joint angle (degrees)			Lateral crus angle (degrees)		Trunk flexion (degrees)	Reference
							Protraction	Retraction	Range	Flexion	Extension	Range	Initial	Maximum		
Skunk (<i>Mephitis</i>)	LS walk	0.28 ms ⁻¹	-	-	-	17	66	-29	95	84	143	59	77	163	-	Goslow and Van De Graaff (1982) (Figs 1, 2)
Opossum (<i>Didelphis</i>)	LS walk	-	-	-	-	-	63	32	31	-	-	-	90	180	-	Jenkins (1971) (Figs 4, 6)
Raccoon	LS walk	1.6-5 km h ⁻¹	-	-	-	12-15†	101	44	57*	65-80*†	-	-	75	157	-	Jenkins and Camazine (1977) (Fig. 1)
Fox	LS walk	1.6-5 km h ⁻¹	-	-	-	10-11†	-	-	59-66*†	-	-	-	-	-	-	Jenkins and Camazine (1977)
Cat	LS walk	1.6-5 km h ⁻¹	-	-	-	5-11†	-	-	69-73*†	-	-	-	-	-	-	Jenkins and Camazine (1977)
Cat	LS walk	-	-	-	64	-	36	-25	61*	78	111	33*	-	-	-	Wetzel <i>et al.</i> (1976) (Fig. 1)
Cat	Walk	2.4 km h ⁻¹	-	0.69	63	-	39	-11	50*	75	112	37*	-	-	-	Goslow <i>et al.</i> (1973) (Tables 3, 4)
Dog	Trot	5.8 km h ⁻¹	-	0.37	43	-	40	-12	52*	59	110	51*	-	-	-	Goslow <i>et al.</i> (1981) (Fig. 8)
Monkey (<i>Cercopithecus</i>)	Walk	3.3 km h ⁻¹	-	0.79	76	-	36	-18	54*	115	150	35*	-	-	-	Vilensky and Gankiewicz (1990) (Fig. 3)
	Trot	8.2 km h ⁻¹	-	-	44	-	15	-45	60*	100	155	55*	-	-	-	
	Walk	0.62 ms ⁻¹	-	-	-	-	39	2	37*	94	139	45*	-	-	-	

Most values have been calculated from figures in the given references. Values for *Dicamptodon* have been included for easy comparison. All angles are in degrees. Femoral angles given have been transformed to match the sign convention used in this study; 0° femoral angle measured from the lateral view indicates the femur perpendicular to the pelvic girdle.

*Indicates that the variables in this group (e.g. femoral angle) were measured from the lateral view.

†Indicates that the value was stated directly in the reference given. All other values were calculated from the reference figures listed.

- A value for this variable was not listed in the reference and could not be calculated from the figures included.

LS walk, lateral sequence walk; CL, carapace length; BL, body length; SVL, snout-vent length; NA, not applicable.

to visualize them. However, it is clear that any travelling wave pattern that emerged would have to be a modified travelling wave, since the amplitude of displacement is reduced in the region of the pelvic girdle, instead of remaining constant, as in some lizards (Ritter, 1992), or increasing down the length of the animal, as in fish (Gray, 1968; Grillner and Kashin, 1976; Videler, 1981).

The location of minimum displacements and flexion angles in the anterior region of the trunk may be related to the salamander's habit of keeping the head pointed in the direction of travel throughout the stride. The damping of oscillations in the head and neck may spill over to the anterior regions of the trunk and, consequently, the amplitude of flexion may likewise be damped in these regions. This same tendency to keep the head pointing forwards has been shown in lizards (Ritter, 1992) and in a marsupial, *Monodelphis domestica*, which also shows lateral bending of the trunk at low speeds (Pridmore, 1992). Steadiness of the head in *Monodelphis* is accomplished by bending of the anterior thoracic vertebrae in the direction opposite to the bending of the rest of the trunk.

In fish that use carangiform locomotion, there is a point of minimum lateral displacement located one-quarter to one-third of the distance down the body, beyond which the amplitude of the travelling wave increases steadily as it passes to the tip of the tail (Grillner and Kashin, 1976; Videler, 1981). This location of minimum displacement roughly corresponds to the position of the pectoral girdle in salamanders (at approximately 25 % of SVL) and also corresponds to the expected location of one of the nodes for a standing wave pattern (Frolich and Biewener, 1992).

It appears that *Dicamptodon* is incapable of using 'pure' travelling waves for locomotion at any speed (short of abandoning the limbs altogether in favour of fast undulatory locomotion). This could be a consequence of relying primarily on the limbs for propulsion, which would require specific configurations of the body at the appropriate times for lifting and placement of the limbs in order to run in a coordinated fashion. The swing phase of the left leg should be started when the trunk is still strongly concave to the right (Fig. 6C) and ended when the trunk is concave to the left, in order to ensure that the distance travelled by the limb during the swing will derive the greatest benefit from the trunk movements. Perhaps introduction of a travelling wave might disrupt this necessary phase-locking of trunk and limb movements, thereby hampering forward speed.

Comparison of limb kinematics with that of other tetrapods

Table 3 provides a summary of values from the literature of angular minima and maxima and excursions for a number of tetrapod taxa. Many of the values presented in this table have been calculated by measuring limb segment angles from figures in the given references. These values must be interpreted with caution, as they represent only one observation, and not a mean value. Variation is often high in kinematic data (Sukhanov, 1974), particularly in what Hildebrand (1966) styled 'poor walkers' or sprawling tetrapods. Nonetheless, comparison of these values, where available, may help to highlight major similarities and differences among tetrapod locomotor systems. These may, in turn, aid in determining which kinematic features of the step cycle may be plesiomorphic for limbed vertebrates (Peters and Goslow, 1983).

The pelvic girdle

Rotation of the pelvic girdle is evident in all of the taxonomic groups given in Table 3 except for turtles and birds. Pelvic girdle rotation is impossible in birds because it is fused into the rigid synsacrum (Gatesy, 1990; Johnston and Bekoff, 1992). Walker (1971) reports no rotation of the pelvic girdle in *Chrysemys*, even though it is not rigidly held in place by the shell. Lizards and crocodylians show the same range of pelvic girdle rotation as salamanders (Table 3). *Monodelphis*, a marsupial mammal, also shows equivalent rotation, of the order of 30–40° (Pridmore, 1992). Available data for other mammals typically reveal a smaller degree of pelvic rotation, which probably correlates with a more upright stance. The pelvic girdle of the skunk rotates approximately 17° (Goslow and Van De Graaff, 1982). Jenkins and Camazine (1977) have shown rotations of the pelvic girdle of 13.5° in raccoon, 10.4° in fox and 7.8° in cat. The mammalian pelvic girdle also undergoes lateral movements during the step cycle, but these movements are generally opposite to the pattern seen in salamanders. Fig. 5 shows that the salamander pelvic girdle moves first away from, then towards, the supporting limb as the stance phase progresses. In contrast, the corresponding movements in skunk (Goslow and Van De Graaff, 1982; Van De Graaff *et al.* 1982), opossum (Jenkins, 1971), raccoon, fox and cat (Jenkins and Camazine, 1977) are *towards* the propulsive leg during early stance phase, then *away* from the propulsive leg later in stance, as the femur retracts and abducts. The two movement patterns probably result from postural differences between the two groups. In mammals, the weight of the body must be balanced over the vertically oriented supporting limb; hence, the movement of the pelvic girdle towards the foot after it is placed on the ground and its subsequent movement to the opposite side after placement of the contralateral foot of the pair. Salamanders, however, may be forced to move the pelvic girdle away from the foot during early stance in order to advance the hip joint; this is because the femur is held parallel to the substratum while rotating about the relatively fixed lower leg.

Protraction and retraction of the femur

Table 3 gives values for the range of femoral protraction and retraction (measured from the dorsal view) that are generally smaller than those measured for *Dicamptodon* (Table 1). Exceptions are *Iguana* and, surprisingly, skunk. The reduced ranges are primarily due to reduced retraction associated with a more upright stance or, in the case of the turtle, to physical restrictions imposed by the shell (Walker, 1971).

Available values for femoral movements measured from the lateral view (Table 3) show ranges similar to those of the salamander (in the dorsal view) in crocodylians and a smaller range in birds and mammals. Again, the smaller range results from less retraction of the femur. Values for femoral protraction are similar in every animal except for the opossum, whose large protraction angle probably results from its tendency to crouch (Jenkins, 1971).

In spite of differences in the degree to which the femur is abducted relative to a parasagittal plane, one of the most constant features of the stance phase in tetrapods is steady femoral retraction, which begins almost immediately after the foot has been placed

on the ground (*Iguana*, Brinkman, 1981; *Caiman*, Brinkman, 1980a; *Alligator*, Gatesy, 1991; skunk, Goslow and Van De Graaff, 1982; Van De Graaff *et al.* 1982; opossum, Jenkins, 1971; Carnivora, Goslow *et al.* 1973, 1981; Wetzel *et al.* 1976; Jenkins and Camazine, 1977; vervet monkey, Vilensky and Gankiewicz, 1990). Birds tend to have a relatively small arc of femoral retraction during walking (Gatesy, 1990; Johnston and Bekoff, 1992), although Gatesy (1990) reports that retraction is abruptly increased once velocity passes a threshold speed.

Knee flexion and extension

Most ranges of motion for the knee joint of the taxa given in Table 3 are similar to the range for *Dicamptodon* (Table 1). Lizards seem to have a somewhat larger excursion, while cursorial mammals show a slightly smaller range. In spite of the general equality of angle ranges for most of the taxa, it should be noted that flexion is greater (i.e. the angle is smaller) for many other taxa than for salamanders, and the amount of extension is correspondingly reduced. The reduced knee joint excursion in cursorial mammals is principally due to a smaller amount of extension in the knee joint.

Two different patterns of knee joint action are seen in the studies listed in Table 3. In one pattern, which is shown by *Dicamptodon*, knee flexion occurs in the first half of the stance phase, and extension begins after the femur has retracted to a position perpendicular to the pelvic girdle. This pattern is seen in *Caiman* (sprawling walk; Brinkman, 1980a), opossum (Jenkins, 1971), various Carnivora (Jenkins and Camazine, 1977), skunk (Goslow and Van De Graaff, 1982; Van De Graaff *et al.* 1982), cat (Goslow *et al.* 1973; Wetzel *et al.* 1976), dog (Goslow *et al.* 1981) and vervet monkey (Vilensky and Gankiewicz, 1990). Mammals typically show a biphasic knee flexion/extension pattern during a stride, with one episode of flexion and extension during the stance phase and another during the swing phase (Goslow *et al.* 1973; Wetzel *et al.* 1976; Goslow and Van De Graaff, 1982; Vilensky and Gankiewicz, 1990). This biphasic pattern may be a consequence of trying to maintain a stable height of the body as it passes over the foot. In contrast, salamanders show a fundamentally uniphasic pattern of flexion beginning in swing phase and continuing through to mid-stance, when extension begins (Fig. 4). A variable, small-amplitude extension/flexion episode at the very beginning of stance is often superimposed on this basic pattern. Birds show yet another variation, with only knee flexion during the stance phase, followed by flexion and then extension during the swing (Gatesy, 1990; Johnston and Bekoff, 1992).

The other general pattern seen in tetrapods is one in which the knee joint is held fixed in early stance and subsequently extends in late stance. All flexion of the knee joint occurs during the swing phase. This pattern is seen in *Iguana* (Brinkman, 1981) and in the high walk of crocodylians (Brinkman, 1980a; Gatesy, 1991).

Positioning of the crus

Initial positioning of the crus divides the animals listed in Table 3 into three groups: those that place the foot ahead of the knee (initial crus angle $<90^\circ$), those that place it directly under the knee ($=90^\circ$) and those that place the foot behind the knee ($>90^\circ$). *Dicamptodon* falls into the first category, along with guinea fowl, skunk and raccoon.

These animals flex the knee in early stance to pull the body forwards on the foot before they thrust the body forwards on the leg. Animals that place the foot essentially under the knee include lizards (excluding *Iguana*), *Alligator*, turtle, chick and opossum. Those that place the foot behind the knee are *Iguana* and *Caiman*. Both of these categories may push the body forwards on the foot throughout the entire stance phase. Maximum elevation of the crus is either the same (*Iguana*, *Basiliscus*, sprawling *Caiman*, *Alligator*, turtle, opossum) or less (high walk *Caiman*, chick, skunk, raccoon) than in *Dicamptodon*.

As in mammals, the crus of salamanders points directly forwards throughout the stance phase. However, unlike mammals, the femur becomes directed laterally in the middle part of the stance phase, which would tend to force the crus to face outwards if the tibia, fibula and metatarsus were immobile. This is the condition in many lizards (Snyder, 1949, 1952; Brinkman, 1981), whose lower limbs do rotate laterally during the stance. In salamanders, the metatarsus does not rotate to point outwards as the limb is retracted, necessitating the tibia and fibula to rotate about their long axes and cross during the stance phase (Schaeffer, 1941).

Plesiomorphic features of the hindlimb step cycle

On the basis of the comparisons presented above, I propose the following features as plesiomorphic for the hindlimb step cycle of tetrapods: (1) rotation of the pelvic girdle through a 30–40° arc (Tables 1, 3), with simultaneous lateral bending of the vertebral column in a standing wave pattern; (2) femoral retraction beginning at the start of stance phase and persisting through stance phase; (3) flexion of the knee in early stance phase pulling the body towards the forwardly placed foot; and (4) extension of the knee joint in late stance phase, after the femur has been retracted past an orientation perpendicular to the pelvic girdle. These features are applicable to the lateral sequence walk, which was undoubtedly used by many groups of primitive tetrapods. The first two movement features are shared by all tetrapod groups, regardless of posture, whereas those relating to knee flexion (movement in a uniphasic pattern) are associated with sprawling postures and are modified (to a biphasic profile) in mammals.

From the available evidence, it is unclear whether other features of the salamander step cycle may be considered to be plesiomorphic. Further studies must be carried out on a larger sample of sprawling-postured tetrapod species (including other salamanders) before any conclusions may be reached on probable hip and knee angle excursions, initial positioning of the crus and possible constraints on the timing of limb movements with axial undulations. This last issue should also be investigated using fish capable of terrestrial locomotion, such as lungfish and walking catfish. Such investigations will further our understanding not only of the likely locomotor capabilities of the earliest tetrapods but also of general mechanisms of integration between locomotor systems.

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