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Limb kinematics during locomotion in the two-toed sloth (*Choloepus didactylus*, Xenarthra) and its implications for the evolution of the sloth locomotor apparatus

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ABSTRACT

In order to gain insight into the function of the extant sloth locomotion and its evolution, we conducted a detailed videoradiographic analysis of two-toed sloth locomotion (Xenarthra: *Choloepus didactylus*). Both unrestrained as well as steady-state locomotion was analyzed. Spatio-temporal gait parameters, data on interlimb coordination, and limb kinematics are reported. Two-toed sloths displayed great variability in spatio-temporal gait parameters over the observed range of speeds. They increase speed by decreasing the durations of contact and swing phases, as well as by increasing step length. Gait utilization also varies with no strict gait sequence or interlimb timing evident in slow movements, but a tendency to employ diagonal sequence, diagonal couplet gaits in fast movements. In contrast, limb kinematics were highly conserved with respect to 'normal' pronograde locomotion. Limb element and joint angles at touch down and lift off, element and joint excursions, and contribution to body progression of individual elements are similar to those reported for non-cursorial mammals of small to medium size. Hands and feet are specialized to maintain firm connection to supports, and do not contribute to step length or progression. In so doing, the tarsometatarsus lost its role as an individual propulsive element during the evolution of suspensory locomotion. Conservative kinematic behavior of the remaining limb elements does not preclude that muscle recruitment and neuromuscular control for limb pro- and retraction are also conserved. The observed kinematic patterns of two-toed sloths improve our understanding of the convergent evolution of quadrupedal suspensory posture and locomotion in the two extant sloth lineages.

1. Introduction

Basic kinematic patterns for fore- and hindlimb movements during symmetrical and asymmetrical quadrupedal locomotion have been published for a broad sample of mammals (e.g., Muybridge, 1887; Manter, 1938; Hildebrand, 1966; Miller and van der Meché, 1975; Hildebrand, 1977; Jenkins and Weijs, 1979; Goslow et al., 1981; Vilensky and Larson, 1989; Gasc, 1993; Fischer, 1994; Rocha-Barbosa et al., 1996; Robert et al., 1999; Schmitt, 1999; Fischer et al., 2002; Schmidt, 2005; Hutchinson et al., 2006; Day and Jayne, 2007; Schmidt, 2008). In principle, these patterns are independent of phylogenetic position, habitat, or anatomical variations from the 'standard mammal' (e.g., reduction or loss of digits or clavicle, presence or absence of long tails). In contrast to the sprawled limb configuration of reptiles and early mammals, which consists of only two propulsive elements (stylopodium and zeugopodium), the therian limb configuration comprises three propulsive elements and one contact element. A proximal element (scapula) was added to the forelimbs, and a distal element (tarsometatarsus) emerged as an individual propulsive element in the hindlimbs (Jenkins and Weijs, 1979; Kuznetsov, 1985; Fischer and Witte, 1998). In symmetrical gaits, more than half of a limb's propulsive moment is produced by retraction of proximal elements (i.e., scapulae and femora). The theoretical prediction of an energy saving, self-stabilizing, three-segmented limb in zig-zag configuration with proximal and distal elements operating in matched motion (pantograph behavior) throughout stance phase is largely fulfilled by therian mammals (Kuznetsov, 1995; Seyfarth et al., 2001; Hackert et al., 2006; Fischer and Blickhan, 2006). Proximal pivots operate at the same height, whereas distal joints predominantly adjust functional limb length to accommodate uneven supports (Fischer et al., 2002). To determine how widespread and adaptive these basic patterns are, non-quadrupeds and/or non-terrestrial species require investigation. This paper presents spatio-temporal gait characteristics and data on inter- and intralimb coordination for two-toed sloths (Xenarthra: *Choloepus didactylus*, Linné 1758) during quadrupedal suspensory locomotion.

Sloth anatomy has been studied extensively (Lucae, 1882; Wislocki, 1928; Britton, 1941; Jouffroy et al., 1962; Goffart, 1971; Mendel, 1979, 1981a,b, 1985a). However, with the exception of

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publications by Mendel concentrating on the autopodia (Mendel, 1981c, 1985b), locomotion-related hypotheses drawn from these descriptions have rarely been tested experimentally. To date, no comprehensive analysis of spatio-temporal or kinematic data of sloth locomotor performance exists.

For quadrupedal suspensory locomotion and postures to be energy efficient, a suite of related morphological adaptations were necessary. Two-toed sloths, unable to lift their trunks from the ground for an extended period of time (Beebe, 1926; Britton, 1941; Mendel, 1981c), evolved hook-like autopodia as well as other adaptations of the musculoskeletal apparatus, especially of limb morphology (Lucae, 1882; Strauss and Wislocki, 1932; Miller, 1935; Jouffroy et al., 1962; Mendel, 1979, 1981a,b, 1985a). These include distal insertions of certain muscles (e.g., *m. brachioradialis* and *m. biceps femoris*) that morphologically maintain flexion of the limbs, requiring activity of the extensors to overcome (Mendel, 1985a), and thus no activity of the flexors against the action of gravity to maintain a flexed limb posture. The morphological adaptations for a sloth-like posture and locomotion are, therefore, profound, a fact which is reflected by the minimal convergent evolution of this posture in other mammalian lineages, despite its benefits. Only extant lorises are able to move in a suspended quadrupedal posture similar to that of sloths (Ishida et al., 1990; Jouffroy and Petter, 1990; Jouffroy and Stern, 1990), although members of the subfossil strepsirhine primate family Palaeopropithecidae are argued to have had sloth-like quadrupedal suspensory postures (Jungers et al., 1991, 1997).

Recent morphological (Gaudin, 2004; Pujos et al., 2007; Gaudin and McDonald, 2008) and molecular (Höss et al., 1996; Delsuc et al., 2001; Greenwood et al., 2001; Poinar et al., 2003; Delsuc and Douzery, 2008) analyses suggest that two- and three-toed sloths (genus *Bradypus*) are only distantly related, a hypothesis first put forward by Patterson and Pascual cited in Webb (1985). Hence their similar quadrupedal suspensory postures resulted from convergent evolution. *Bradypus* is argued to be either the sister group to all other extinct and extant sloths (Gaudin and McDonald, 2008) or, according to most molecular phylogenies, to be associated with the extinct megatherid sloths (Höss et al., 1996; Greenwood et al., 2001). *Choloepus* is regarded as a member of the Megalonychidae, a group comprising primarily extinct 'ground sloths' from North America (McDonald and DeIuliis, 2008). Whatever the case, it is likely that suspensory quadrupedalism evolved independently in the lines leading to extant sloths.

The aims of this paper are to: (i) provide a detailed description of *Choloepus* locomotor kinematics in order to understand whether, and if so, how the quadrupedal suspensory locomotion of two-toed sloths deviates from the basic limb kinematics of therian mammals besides being inverted, (ii) contribute to the understanding of the convergent evolution of suspensory posture and locomotion of sloths, and (iii) provide a baseline study for further investigations of the musculoskeletal system of sloths.

2. Materials and methods

2.1. Study design and study subjects

We conducted two basic locomotion analyses. First we analyzed the unrestrained locomotion of two-toed sloths to gauge speed-related aspects of spatio-temporal and kinematic parameters, and to determine a suitable speed range for a detailed kinematic analysis in the subsequent steady-state locomotion analysis. In both basic analyses we used high-speed standard light videography and videoradiography (see below). As an additional heuristic tool we developed an animated 3D model based on computer tomography reconstruction and kinematic data from videoradiography which made whole-body skeletal motions visible from any desired perspective (Fischer et al., 2010).

(1) Unrestrained locomotion was filmed (a) using a Photron Fastcam-X 1024 PCI (Photron USA, Inc., San Diego, CA, USA) during daily habituation to assess spatio-temporal gait parameters and interlimb coordination and (b) using a biplane X-ray facility at the Klinik für Interventionelle und Diagnostische Radiologie of the university hospitals of the Friedrich-Schiller-Universität Jena, Germany to assess speed-dependent effects of intralimb kinematics. During daily habituation sloths were filmed as they moved freely along a horizontal wooden pole 4.2 m long and 40 mm in diameter. Mendel (1981a,b) speculated that sloth locomotion was most efficient on supports of about this diameter. Locomotion was recorded at 125 frames per second (fps). The camera was positioned perpendicular to the direction of travel. Videoradiographic recordings from the lateral and dorso-ventral perspective were made at 30 fps as the sloths passed 40 cm and 28 cm image intensifiers, respectively, at their own preferred speeds. Because the animals were large relative to the size of the image intensifiers, only parts of a limb moving through its step cycle could be recorded. However, we recorded a sufficient number of trials to obtain at least 30 shots of individual joints and elements at instants of touch down, mid-contact, lift off, and mid-swing to assess speed-related kinematic effects.

(2) In the steady-state locomotion analysis, spatio-temporal gait parameters, interlimb coordination data, and intralimb coordination data were recorded simultaneously. We used the recently established high-speed videoradiography facility of our institute. The digital system is based on the high-end X-ray device Neurostar (Siemens AG, Erlangen, Germany), which we, in collaboration with Siemens AG, adjusted to our needs. It allows synchronous biplane videoradiographic recordings on two 40 cm image intensifiers and the recording of two additional synchronous standard light high-speed cameras. Sloth locomotion was recorded at 300 fps using maximum resolution (1536 × 1024 pixels). To ensure steady-state locomotion, sloths were trained to move along a motorized 4 m long 'treadpole', the equivalent to an arboreal treadmill. The speed of the 'treadpole' was continually adjusted to keep the sloths in front of the image intensifiers for as long as possible. That is, 'treadpole' speed was adjusted to that preferred by the animals. Subsequently, only trials with speeds between 0.2 m/s and 0.3 m/s were analyzed. Trials which were slower or faster than this were discarded, as were trials in which the subjects obviously braked or accelerated. The selected speed range (1) enabled sloths to stride uniformly and (2) was regarded to yield uniform kinematics upon analysis of the unrestrained locomotion analysis. Keeping the animals in front of the two image intensifiers with help of the 'treadpole' allowed us to simultaneously record the movements of the skeletal elements from dorso-ventral and lateral perspectives. Videoradiographic recordings were made at 55–75 kV and 28–75 mA depending on the thickness of the body region of interest and the body properties of the subjects. Parallax was corrected by calibration of the recordings before data analysis. In addition to these 'anatomical close-ups', we used the synchronous standard light high-speed recordings to assess spatio-temporal gait parameters and interlimb coordination of the steady-state analysis. To this end one of the standard light cameras was positioned perpendicular to the 'treadpole'.Three of four adult subjects available for the study were successfully trained to move on the different experimental setups. The training period necessary for the animals to get accustomed to the setups varied between subjects but generally was longest for the 'treadpole' setup (up to six months). Sub-