

Role of the Prehensile Tail During Ateline Locomotion: Experimental and Osteological Evidence

Daniel Schmitt,^{1*} Michael D. Rose,² Jean E. Turnquist,³ and Pierre Lemelin⁴

¹*Department of Biological Anthropology and Anatomy, Duke University, Durham, North Carolina 27710*

²*Department of Radiology, New Jersey Medical School, University of Medicine and Dentistry of New Jersey, Newark, New Jersey 07101*

³*Department of Anatomy, Medical Sciences Campus, University of Puerto Rico, San Juan, Puerto Rico 00936*

⁴*Division of Anatomy, Faculty of Medicine and Dentistry, University of Alberta, Edmonton, Alberta T6G 2H7, Canada*

KEY WORDS *Ateles*; brachiation; caudal vertebrae; kinematics; *Lagothrix*; prehensile tail; tail-assisted brachiation

ABSTRACT The dynamic role of the prehensile tail of atelines during locomotion is poorly understood. While some have viewed the tail of *Ateles* simply as a safety mechanism, others have suggested that the prehensile tail plays an active role by adjusting pendulum length or controlling lateral sway during bimanual suspensory locomotion. This study examines the bony and muscular anatomy of the prehensile tail as well as the kinematics of tail use during tail-assisted brachiation in two primates, *Ateles* and *Lagothrix*. These two platyrrhines differ in anatomy and in the frequency and kinematics of suspensory locomotion. *Lagothrix* is stockier, has shorter forelimbs, and spends more time traveling quadrupedally and less time using bimanual suspensory locomotion than does *Ateles*. In addition, previous studies showed that *Ateles* exhibits greater hyperextension of the tail, uses its tail to grip only on alternate handholds, and has a larger abductor caudae medialis muscle compared to *Lagothrix*. In order to

investigate the relationship between anatomy and behavior concerning the prehensile tail, osteological data and kinematic data were collected for *Ateles fusciceps* and *Lagothrix lagothricha*. The results demonstrate that *Ateles* has more numerous and smaller caudal elements, particularly in the proximal tail region. In addition, transverse processes are relatively wider, and sacro-caudal articulation is more acute in *Ateles* compared to *Lagothrix*. These differences reflect the larger abductor muscle mass and greater hyperextension in *Ateles*. In addition, *Ateles* shows fewer side-to-side movements during tail-assisted brachiation than does *Lagothrix*. These data support the notion that the prehensile tail represents a critical dynamic element in the tail-assisted brachiation of *Ateles*, and may be useful in developing inferences concerning behavior in fossil primates. *Am J Phys Anthropol* 126:435–446, 2005.

© 2004 Wiley-Liss, Inc.

A clear understanding of the relationship between anatomy and behavior in living animals is critical for the development of sound inferences concerning the behavior of extinct primates. In this paper, the relationship between form and function of the prehensile tail in two closely related, but behaviorally distinct platyrrhine monkeys is examined. These data could help infer prehensile tail use in fossil atelines such as *Protopithecus* and *Caipora* (Cartelle and Hartwig, 1996; Hartwig and Cartelle, 1996) and help in understanding suspensory behavior in tailless Miocene catarrhines (Rose, 1983, 1989, 1994).

Bimanual suspensory locomotion is rare among mammals, but appears to have evolved at least twice among primates, i.e., in platyrrhines and hominoids. Although the mechanics of bimanual suspensory locomotion in *Ateles* (which includes tail-assisted bra-

Grant sponsor: National Science Foundation; Grant number: SBR-9222526; Grant sponsor: School of Medicine of the University of Puerto Rico; Grant sponsor: National Center for Research Resources; Grant number: Research Centers in Minority Institutions RR-03051; Grant sponsor: National Institutes of Health; Grant sponsor: L.S.B. Leakey Foundation.

*Correspondence to: Daniel Schmitt, Department of Biological Anthropology and Anatomy, Duke University Medical Center, Box 3170, Durham NC 27710.

Received 17 December 2002; accepted 12 January 2004.

DOI 10.1002/ajpa.20075

Published online 8 September 2004 in Wiley InterScience (www.interscience.wiley.com).



Fig. 1. Video image of *Ateles fusciceps robustus*, showing position of forelimb and tail during tail-assisted brachiation.

chiation, as shown in Fig. 1) and *Hylobates* are superficially similar, they exhibit a number of differences.¹

¹The categorization of locomotor modes used here utilizes and adds to that of Hunt et al. (1996). Bimanual suspensory locomotion involves alternate handholds during forward progression. Brachiation and forelimb-swinging are types of bimanual suspensory locomotion. The brachiation of hylobatids involves marked trunkal rotation and a relatively long free-flight phase, complete extension at the elbow joint, abduction at the shoulder joint, and flexion at the hip and knee joints. The tail-assisted brachiation of atelines involves less extensive trunkal rotation, a relatively brief free-flight phase, little or no flexion of the hindlimbs, and prehensile use of the tail (Carpenter and Durham, 1969; Chang et al., 1997; Fleagle, 1976; Jungers and Stern, 1981, 1984). Forelimb-swinging, also practiced by atelines (Cant et al., 2003), involves even less trunkal rotation and the absence of a free-flight phase. It is sometimes accompanied by more flexion at the elbow (flexed-elbow forelimb-swinging). In the text, the terms "tail-assisted brachiation," "bimanual suspensory locomotion," and "suspension" are used advisedly, depending on the generality of the point being introduced.

It was suggested that the differences in kinematics of bimanual suspensory locomotion between *Ateles* and *Hylobates* are primarily related to the use of the prehensile tail by the former. Lewis (1969, 1971) proposed that the prehensile tail of *Ateles* passively limits trunkal rotation. Stern et al. (1980) and Jungers and Stern (1981) suggested that the prehensile tail serves primarily as a "fail-safe mechanism" for the mechanically less specialized "brachiation" of *Ateles*. Other studies, however, suggest that this view of the tail as a passive restraint may be an oversimplification. Several authors noted that the tail of *Ateles* typically contacts the support only on alternate hand-holds, and that the prehensile tail of *Ateles* may be used to control pendular motion and lateral body sway during locomotion (Carpenter and Durham, 1969; Turnquist, 1975; Jenkins et al., 1978; Lemelin, 1995; Turnquist et al., 1999).

Additional data are needed to more fully understand the mechanical role of the prehensile tail in atelines. To attempt to fill this gap in knowledge, myological, osteological, and kinematic aspects of the prehensile tail were examined in two closely related but ecologically distinct atelines, *Ateles* and *Lagothrix*, which both utilize tail-assisted brachiation.

SUSPENSORY LOCOMOTION IN ATELES AND LAGOTHRIX

A prehensile tail is advantageous for hanging during feeding in the canopy, and is used in this fashion by several platyrrhine species (Carpenter and Durham, 1969; Durham, 1975; Mittermeier and Fleagle, 1976; Mittermeier, 1978; Fleagle and Mittermeier, 1980; Cant, 1986; Lemelin, 1995; Garber and Rehg, 1999). How a prehensile tail is used during locomotion is not well documented and it is unknown whether the functional role of the tail varies within prehensile-tailed, suspensory primates.

Ateles and *Lagothrix* are both large-bodied platyrrhines (between 7–9 kg) that move using a combination of climbing, clambering, quadrupedalism, and suspension (Carpenter and Durham, 1969; Durham, 1975; Mittermeier, 1978; Fleagle and Mittermeier, 1980; Defler, 1999; Cant et al., 2001). Nonetheless, these genera differ in ways that may significantly impact on the use of the prehensile tail during tail-assisted brachiation. *Lagothrix* has a lower intermembral index and a much shorter forelimb relative to trunk length compared to *Ateles* (Erickson, 1963; Jungers, 1985). These proportional differences are associated with differences in the frequency of bimodal suspensory locomotion in these two genera (Carpenter and Durham, 1969; Durham, 1975; Defler, 1999). In a field study of suspensory locomotion, Cant et al. (2001) found that *Ateles* uses suspensory modes during travel twice as much as *Lagothrix*. In addition, when this mode is further subdivided, *Ateles* uses “full-stride brachiation” 2.4 times as much as *Lagothrix* (Cant et al., 2003).

A kinematic study of captive *Ateles* and *Lagothrix* conducted by Turnquist et al. (1999) demonstrated that *Lagothrix* used its tail with every handhold and, when compared to *Ateles*, took relatively short, choppy strides which did not extend the arc of the swing to its full potential (Fig. 2). Turnquist et al. (1999) also noted that compared to *Lagothrix*, *Ateles* showed significantly greater degrees of tail hyperextension (tail arched forward), particularly when the tail was not in contact with the support (Fig. 2).

OSTEOLOGY OF THE PREHENSILE TAIL

Based on previous studies (Schultz, 1961; Ankel, 1962, 1963, 1972; German, 1982; Rosenberger, 1983; Lemelin, 1995; Meldrum, 1998), major osteological differences between prehensile tails and nonprehen-

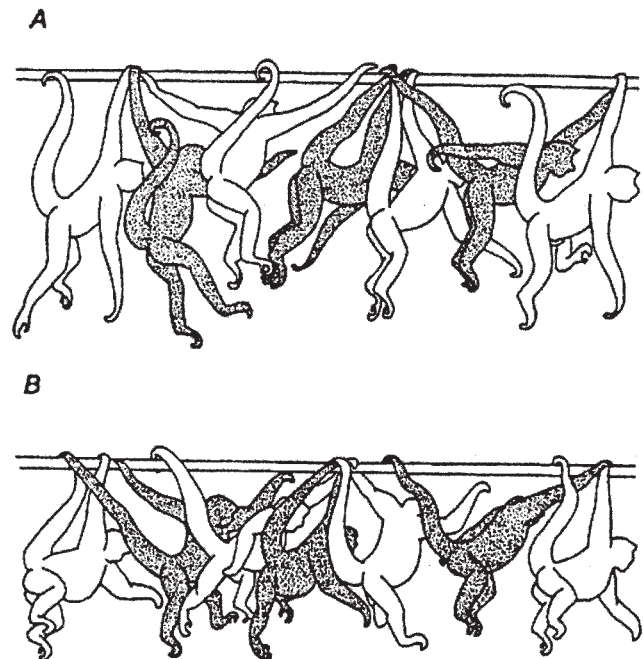


Fig. 2. Tracing taken from videorecordings of typical tail-assisted brachiation sequences of (A) *Ateles* and (B) *Lagothrix* (from Turnquist et al., 1999). Note that tail of *Lagothrix* is in nearly constant contact with pole, whereas *Ateles* uses its tail every other handhold. In addition, tail of *Ateles* is characterized by much more acute tail-body angles than those of *Lagothrix*.

sile tails of primates are shown in Figure 3 and summarized below. Although the description below focuses on primates, Youlatos (2003) found similar differences between prehensile tails and nonprehensile tails in carnivorans.

The prehensile tail of atelines is relatively longer than the nonprehensile tail of other primates. Prehensile tails have, on average, more caudal vertebrae than nonprehensile tails, and each caudal element appears to be, on average, shorter relative to overall tail length. In addition, the more distal caudal vertebrae of prehensile-tailed atelines have relatively wider transverse processes compared to those of nonprehensile-tailed species, possibly reflecting the larger loads on the tail and larger tail musculature (German, 1982; Lemelin, 1995; Meldrum, 1998).

The size of the caudal vertebrae gradually increases in length in the proximal third of the tail, and then gradually decreases all the way to the tip of the tail, allowing the tail to be divided into distinct proximal and distal regions. In the proximal tail region, the first 4–7 caudal vertebrae (depending on the species) have neural arches, lumbar-like zygapophyseal articulations, and a single pair of transverse processes. The last caudal vertebra in the proximal tail segment represents the “transitional vertebra” (Ankel, 1972; German, 1982), which has zygapophyseal articulations only on the proximal (cranial) portion and may have either one or two

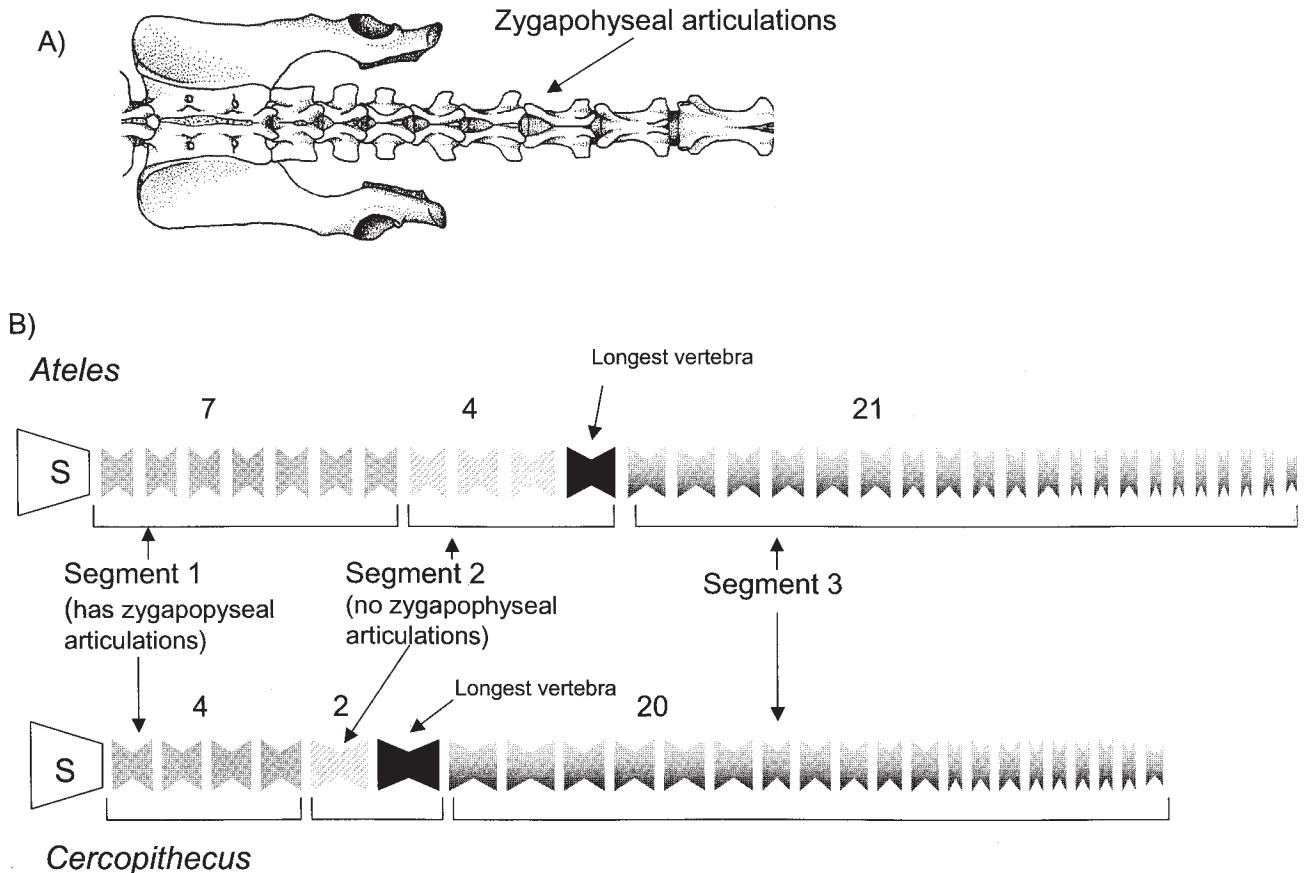


Fig. 3. A: Dorsal view of proximal tail region in *Lagothrix*. Vertebrae in first segment have zygapophyseal articulations. Transitional vertebra (as defined by Ankel, 1972) has zygapophyseal articulations on proximal end only. **B:** Schematic diagram (based on Ankel, 1972) of prehensile tail (*Ateles*) and nonprehensile tail (*Cercopithecus*). S, sacrum. Tail of primates has been traditionally divided into two regions, with transitional vertebra dividing them. Here, longest vertebra divides traditional distal region of tail into two distinct segments. As noted in text, division of tail into three segments allowed for more subtle functional comparison between species. Segment 1 is in dark gray and includes transitional vertebra. Segment 2 is in hatched light gray and includes longest caudal vertebrae (black). Segment 3 is in graded light gray. Prehensile tail of *Ateles* is longer, with more numerous, relatively shorter elements.

pairs of transverse processes. The caudal vertebrae in the distal tail region have no zygapophyseal articulations and two pairs of transverse processes. This region of the tail can be further divided into two segments: a more proximal segment from the transitional vertebrae to, and including, the longest vertebrae, and a more distal segment that includes all remaining vertebrae which decrease in size and complexity.²

These differences in the number and size of vertebrae have clear functional implications for the

range of flexion and extension that can be achieved by the tail. A chain made up of more numerous, shorter elements has greater flexibility and can be bent into more acute angles compared to a tail with fewer longer elements (Fig. 4).

Very little is known concerning the osteological correlates of tail use between *Ateles* and *Lagothrix*. Based on osteological differences between prehensile tails and nonprehensile tails of primates and kinematic differences in tail extension, it is predicted that *Ateles* should have more numerous, relatively shorter caudal vertebrae in the first segment of the tail compared to *Lagothrix*. Along with changes in the number and size of caudal elements, differences in tail extension may be reflected in the sacro-caudal articulation angle between both ateline species.

MYOLOGY OF THE PREHENSILE TAIL

The study by Lemelin (1995) of the tail musculature of prehensile and non-prehensile-tailed primates revealed that *Lagothrix* and *Ateles* differ

²Although previous studies divided the tail into two regions, we found it useful to divide the tail into three segments: 1) a proximal segment including all caudal vertebrae with zygapophyseal articulations and the transitional vertebra, which traditionally divides the tail into proximal and distal regions; 2) a middle segment consisting of caudal vertebrae without zygapophyseal articulations (located distal to the first tail segment) all the way and including the longest caudal vertebra; and 3) a distal segment consisting of all remaining caudal vertebrae. This division into three segments allowed for a subtler and more detailed functional comparison, because morphological changes in each region impact differently on the mechanics of the tail (Figs. 3, 9).

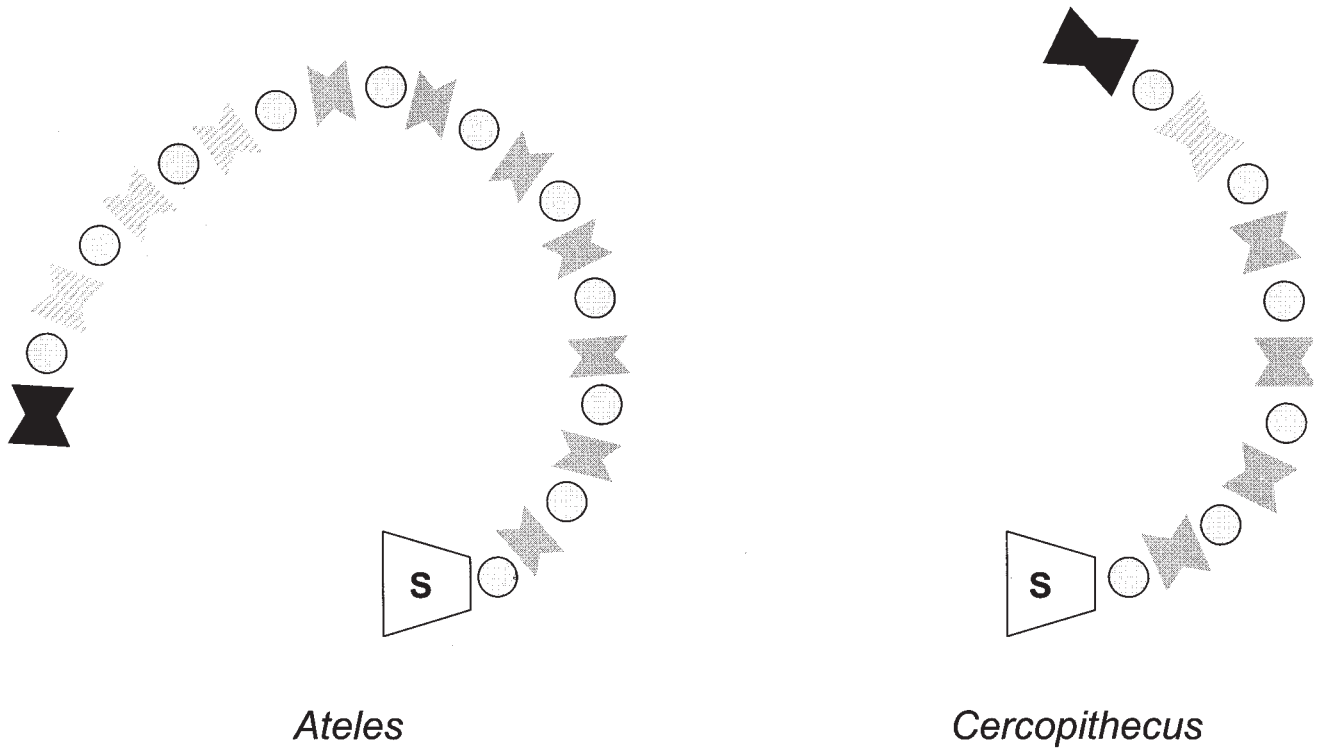


Fig. 4. Schematic diagram of effect of having numerous, relatively short elements in a chain. S, sacrum. Black section indicates longest vertebra. Circles represent articular discs between vertebrae. Prehensile tail of *Ateles* (left) has greater flexibility and can develop tighter curvatures and higher degrees of extension compared to nonprehensile tail of *Cercopithecus* (right).

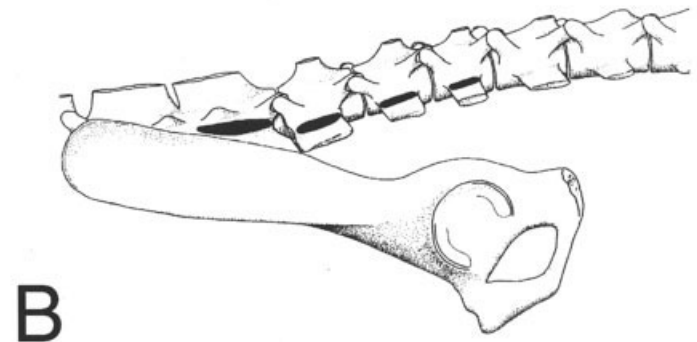
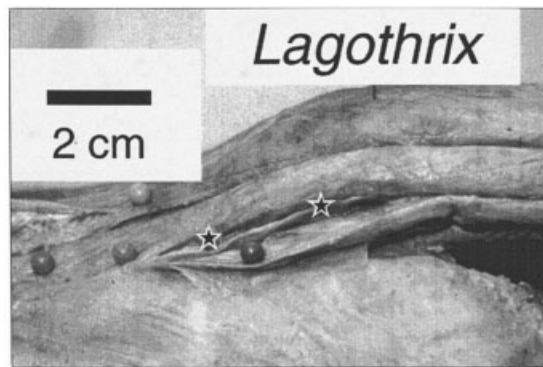
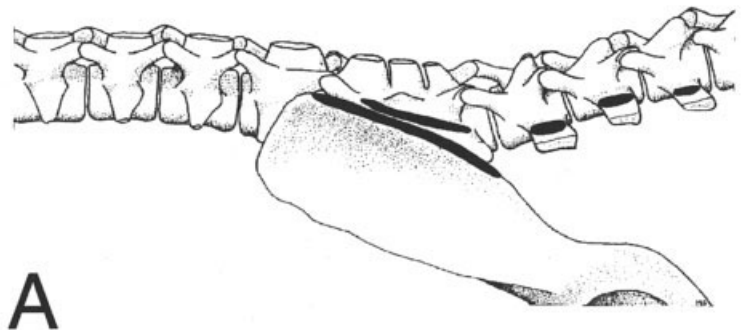
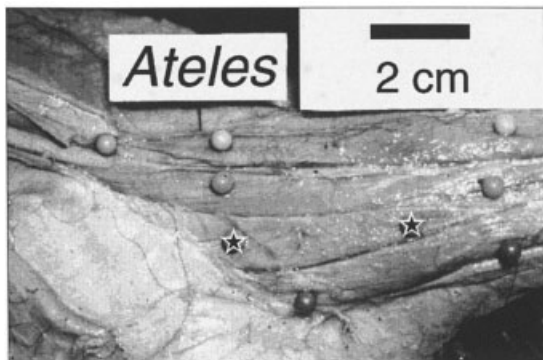


Fig. 5. Differences in size and attachment of abductor caudae medialis muscle between (A) *Ateles* and (B) *Lagothrix* (modified from Lemelin, 1995). Left: Dorsolateral views of musculature at base of tail, with abductor caudae medialis muscle indicated by stars. This muscle is larger in *Ateles* (A) and has broad attachment on ilium compared to *Lagothrix* (B), where it is a small slip of muscle with limited attachment as indicated by black shading on drawings of tail skeletons at right.

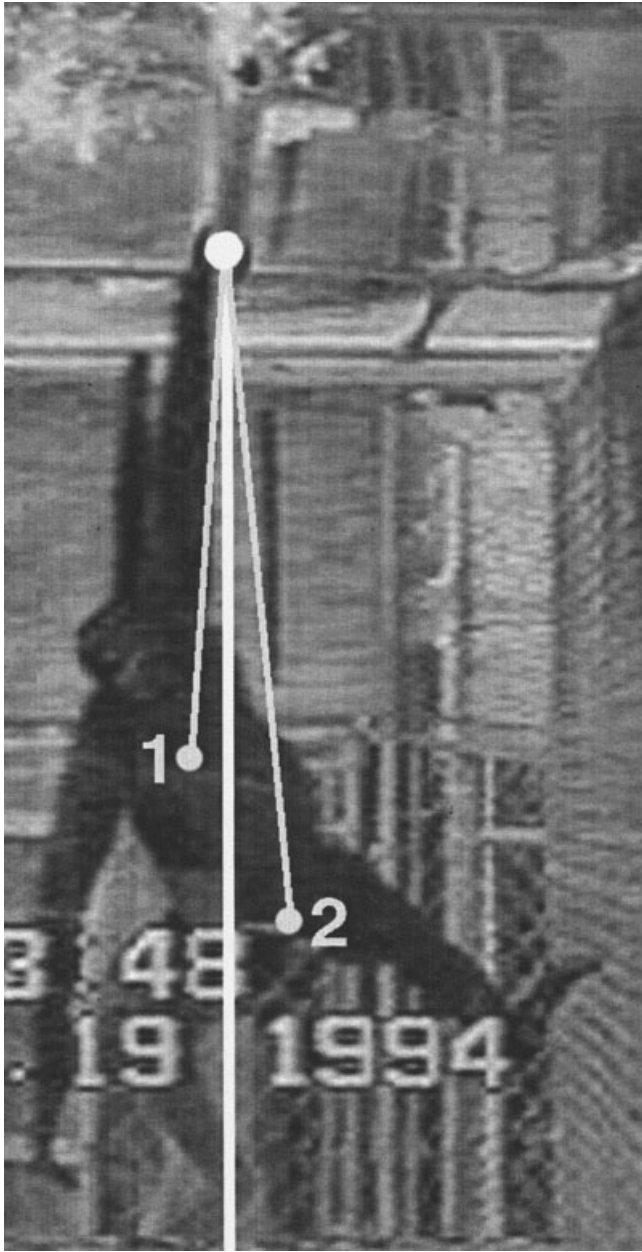


Fig. 6. Angles of displacement of chest (1) and groin (2) from a vertical axis dropped from point of handhold on overhead support.

markedly in the extent and relative development of the abductor caudae medialis muscle. In *Ateles*, this muscle is large with a broad fleshy origin on both the sacrum and ilium (Fig. 5A). Its extensive insertion fills much of the available surface area on the transverse processes of the proximal caudal vertebrae in the first segment of the tail (Fig. 5A). In contrast, this muscle in *Lagothrix* is only a thin slip with no attachment on the ilium (Fig. 5B).

It is likely that the main action of the abductor caudae medialis is abduction of the tail at its base. However, the functional role of this muscle, particularly in *Ateles*, may be quite different. Both Carpenter and Durham (1969) and Jenkins et al. (1978)

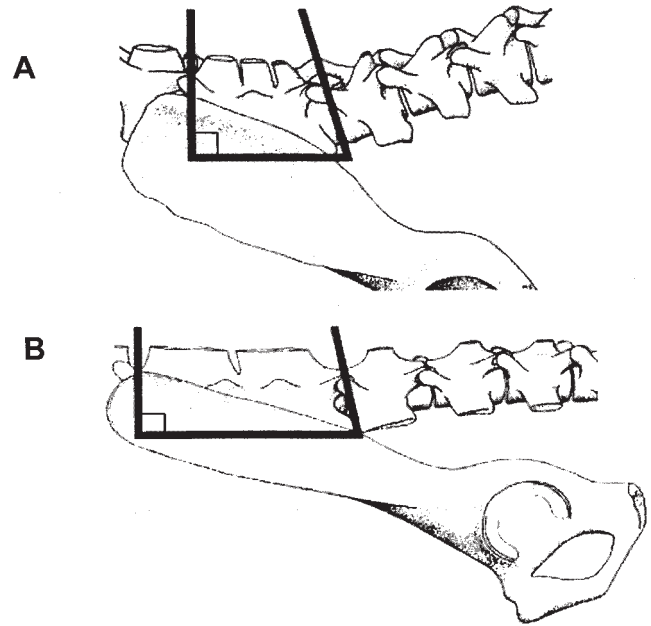


Fig. 7. Angle of centrum facet for articulation of sacrum with first caudal vertebra in (A) *Ateles* and (B) *Lagothrix*. This angle is measured relative to an axis perpendicular to plane of proximal (lumbar) articular surface of sacrum. Actual measurements were made on disarticulated, isolated sacra.

suggested that *Ateles* may use its tail to control lateral sway of the body under the support. On that basis, Lemelin (1995) proposed that when the tail is grasping a support, and is therefore fixed at its distal end, the abductor caudae medialis muscle may act to control sway at the base of the tail. He further suggested that in this position, the abductor caudae medialis muscle could also “stabilize the base of the tail during arm-swinging to counteract lateral excursions of the center of gravity” (Lemelin, 1995, p. 365–366).

Muscular differences between *Ateles* and *Lagothrix* suggest two other associated differences. First, it is likely that proximal caudal vertebrae in *Ateles* will require expanded surface areas to support the large musculature. Second, *Ateles* and *Lagothrix* should exhibit different amounts of lateral sway during tail-assisted brachiation.

MATERIALS AND METHODS

Three different sources of data (osteological, myological, and behavioral) are utilized in this study to address the question of form and function. As a result, sample sizes, sources of material, and statistical analyses vary greatly within the study. For example, although a large amount of osteological material was available, fewer cadavers and still fewer live specimens were available. Clearly, a sample size of one individual *Lagothrix* and *Ateles* cannot describe intraspecific variation. The kinematic data are used as a preliminary test of hypotheses derived from the anatomical studies.

The kinematics of tail-assisted brachiation in *Ateles fusciceps robustus* and *Lagothrix lagothricha lugens* were studied from videotapes of one adult male of each species at the DuMond Conservancy/Monkey Jungle (Miami, FL). The housing, experimental enclosure, and filming techniques were described in detail elsewhere (Turnquist et al., 1999), and are only briefly summarized here.

Bouts of tail-assisted brachiation were recorded in a specially designed enclosure ($7.8 \times 1.7 \times 2.1$ m) with clear Lexan panels (2.5×6.4 m) on the side, top, and end. The animals traveled along a 6.4-m section of 3.5-cm galvanized steel pipe suspended on steel brackets 0.3 m below the ceiling. Three electronically shuttered (1/1,000 sec) CCD cameras recording at 60 images/sec were positioned lateral to, overhead from, and in line (frontal) with the line of travel. The tapes were synchronized using both a series of photocells with LED lights and an audio track recorded on all videotapes simultaneously. Videotapes were reviewed, and only steps with continuous motion across the enclosure with no obvious acceleration or deceleration were used for analysis. The first and last steps of a locomotor bout were never used. All sequences involved three or more strides down the length of the enclosure. Only those steps in which the subject was in the middle portion of the cage were used. Only one stride per locomotor bout (travel down the enclosure) was used. Twenty strides for *Ateles* and 16 strides for *Lagothrix* were selected for analysis from the videotapes of the frontal camera. The sample for *Ateles* could further be divided into 13 strides for which the tail was not on the substrate, and 7 strides for which the tail was on the substrate.

Images from the frontal camera only were used to determine the amount of lateral sway of the body. Frontal view sequences were analyzed on a Macintosh G3 computer, using MacMorph software (Spencer and Spencer, 1995). The frontal sequences include bouts both when the animal is swinging towards the camera and when the animal is traveling away from the camera. During tail-assisted brachiation, angular measurements were taken at the lowest possible point of the swing in the direction of movement along the branch. This maximum depth of swing correlated closely to both midsupport and the point of largest lateral deviation (Turnquist et al., 1999).

On frontal view recordings, angles were measured to determine the maximum amount of lateral sway (i.e., lateral displacement of the body) experienced during a stride. The angles measured are illustrated in Figure 6. A vertical line dropped from the point of the handhold to the floor of the enclosure was superimposed onto the video image as a reference plane. Using the handhold as an axis of rotation, angles were then measured between this line and two points on the animal's body (chest and groin) in order to evaluate sway (deviation) from the vertical. These two angles not only measure body sway but

TABLE 1. Angular measure (in degrees) of lateral sway during bimanual suspensory locomotion from vertical between *Ateles* and *Lagothrix*¹

	<i>Lagothrix</i> (N = 20)	<i>Ateles</i> using tail (N = 7)	<i>Ateles</i> not using tail (N = 13)
Chest-vertical	25.1 (8.8)	4.1 (0.9)	8.2 (2.7)
Groin vertical	15.6 (9.1)	4.9 (2.8)	9.0 (3.6)

¹ Mean and 1 standard deviation (in parentheses). All comparisons (*Lagothrix* vs. *Ateles* with tail, *Lagothrix* vs. *Ateles* without tail, and *Ateles* with tail vs. *Ateles* without tail for both angles) were significant at $P < 0.05$, using Mann-Whitney U-test.

also provide information on body angulation and the position of the body as a whole relative to the support. Both values were taken for all strides.

The first angle, the "chest-vertical" angle, was measured by digitizing a point on the chest (or back) corresponding to the point on the midline of the body in the center of the chest approximately mid-sternum. The angle between the line from this chest point to the handhold and the vertical line was then calculated. Thus, the "chest-vertical" angle measures the amount of lateral sway at midsupport of the upper thorax from the vertical plane.

The second angle, the "groin-vertical" angle, was measured by digitizing a point corresponding to the lowest point (groin) on the body midway between the two hips. The angle between the line from the groin point to the handhold and the vertical line was calculated. Thus the "groin-vertical" angle represents the amount of lateral sway at midsupport of the groin away from the vertical plane.

All statistics were computed using SAS statistical software for PCs (SAS Institute, Cary, NC). Because the sample is small, conservative nonparametric pairwise comparisons were used. Maximum chest and groin sways were compared across species, using a Mann-Whitney U-test (Sokal and Rohlf, 1981). In addition, these same variables were compared within *Ateles* when the tail was grasping the substrate compared to when the tail was not. Each of these conditions in *Ateles* was also compared separately to *Lagothrix*.

Osteological data included measurements of all tail segments as well as individual vertebrae. Data were collected (by M.D.R.) from skeletons with complete tails. Specimens were from the collections of the following institutions: the American Museum of Natural History (New York, NY), Anthropologisches Institut und Museum (Zürich, Switzerland), Field Museum (Chicago, IL), Instituto Pau Brasil (Aruja, Brazil), Museu de Ciências Naturais (Belo Horizonte, Brazil), Museu de Zoologia (São Paulo, Brazil), Museu Nacional (Rio de Janeiro, Brazil), National Museum of Natural History (Washington, DC), and Natural History Museum (London, UK). Measurements on the number and length of caudal vertebrae included: 1) relative tail length defined as the summed cranio-caudal length of all caudal vertebrae from all three segments divided by the

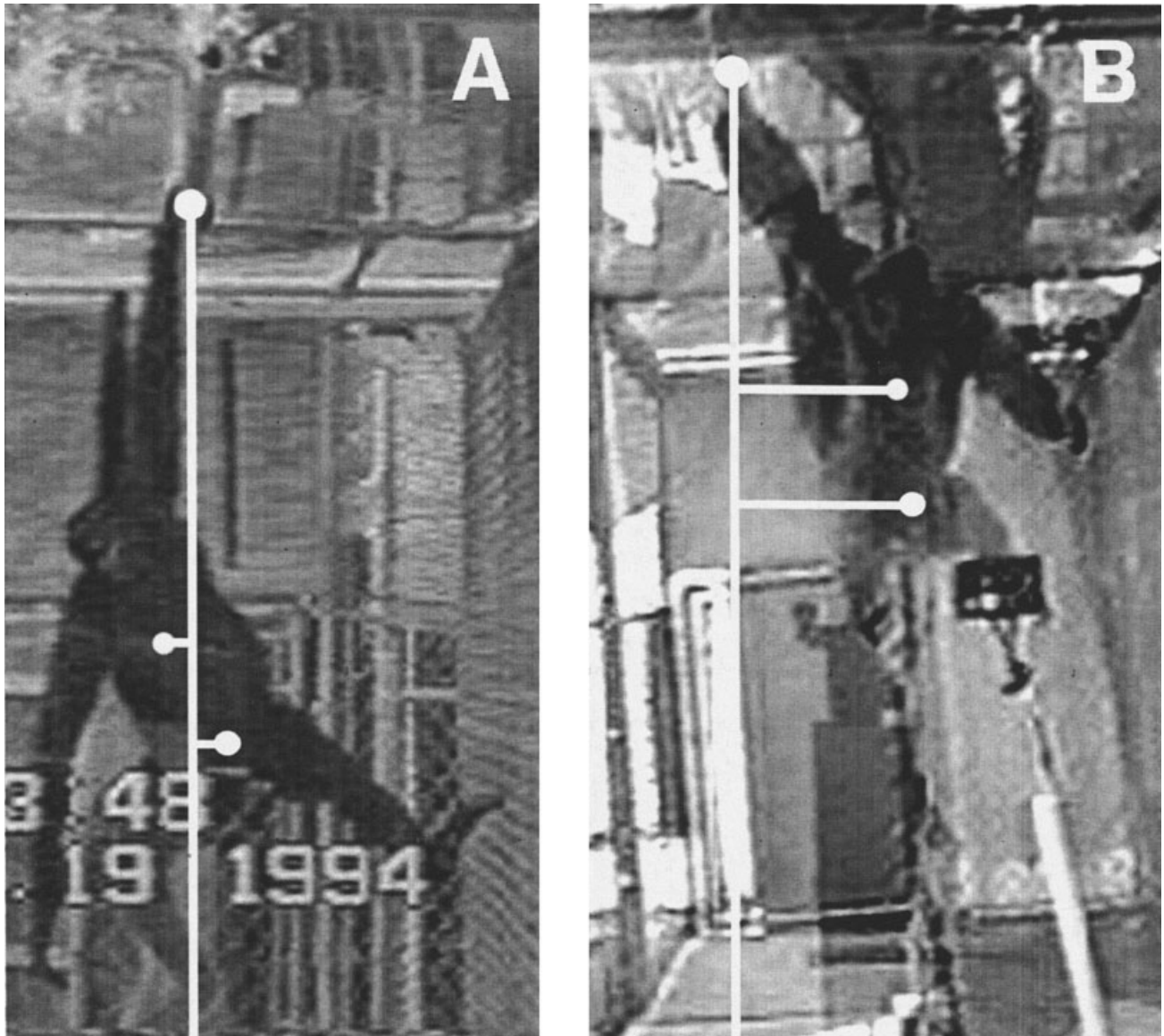


Fig. 8. Comparison of lateral sway of body in *Ateles* (A) and *Lagothrix* (B). During tail-assisted brachiation, body of *Ateles* deviates very little from vertical, whereas body of *Lagothrix* is displaced far to side of vertical. Note in *Ateles* that chest and groin deviate in opposite directions from vertical, while in *Lagothrix*, they deviate to same side.

summed length of all thoracolumbar (trunk) vertebrae; 2) number of caudal vertebrae (all three segments together); 3) average relative length of caudal vertebrae defined as 100 divided by the number of caudal vertebrae (for comparison with measurement 6); 4) relative length of the first segment defined as the first segment length divided by the total tail length; 5) number of caudal vertebrae in the first segment; and 6) average relative length of caudal vertebrae in the first segment defined as 100 times the length of the first segment divided by the number of vertebrae in the first segment and then divided by tail length.

A seventh measurement designed to look at the natural angle (in degrees) of flexion of the tail on the sacrum (sacro-caudal angle) was calculated on an isolated sacrum as the angle at the intersection of

the plane of the centrum facet for articulation with the first caudal vertebrae with an axis perpendicular to the plane of the proximal (lumbar) articular surface of the sacrum (Figs. 7, 11). The sample size for these seven variables was 20 adult individuals each of *Lagothrix* and *Ateles*.

Finally, the area available for tail musculature in *Ateles* and *Lagothrix* was also analyzed by comparing transverse process width relative to vertebral centrum width in *Ateles* and *Lagothrix*. This index is 100 times the transverse width between the tips of transverse processes minus the transverse width of the cranial face of the centrum divided by two, and then this value is divided by the transverse width of the cranial face of the centrum. This describes the relative width of one transverse process against centrum width. The

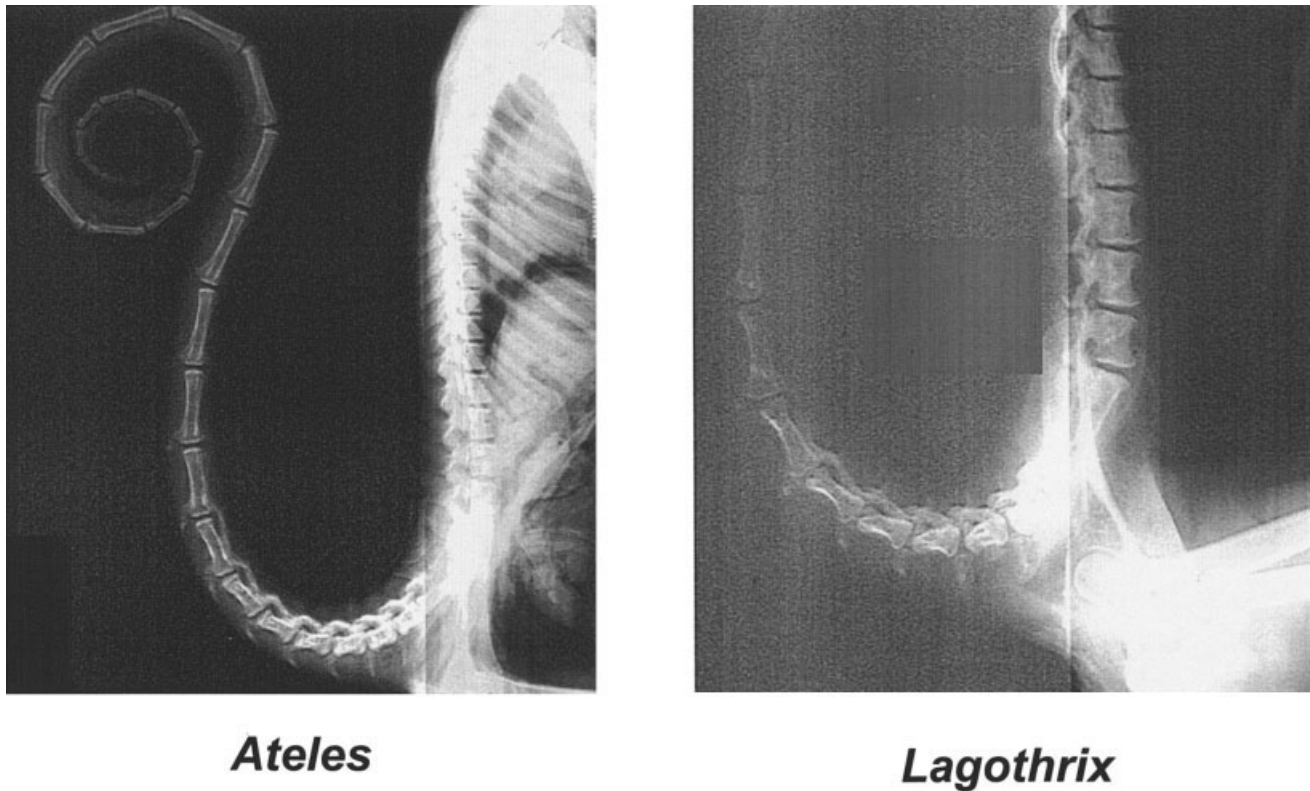


Fig. 9. Radiographs of spine and tail of *Ateles* and *Lagothrix*. Tails in radiographs are arranged to demonstrate morphological rather than kinematic differences. They are placed in roughly same degrees of curvature and extension.

TABLE 2. Metric differences between caudal vertebrae of *Ateles* and *Lagothrix*¹

	<i>Ateles</i> (N = 20)	<i>Lagothrix</i> (N = 20)
Average number of caudal vertebrae (all segments)	32.1 (1.2)	29.9 (0.72)
Average relative caudal vertebrae length (all segments)	3.1 (0.12)	3.3 (.08)
Average number of caudal vertebrae in segment 1	7.1 (0.75)	5.2 (0.62)
Average relative caudal vertebrae length in segment 1	2.5 (0.16)	2.7 (0.17)

¹ Mean and 1 standard deviation (in parentheses). All cross-species comparisons significantly different at $P < 0.001$, using two-tailed t -tests.

sample size for this index was 12 individuals of *Ateles* and 16 individuals of *Lagothrix*.

Statistical tests were carried out to compare values for *Ateles* vs. *Lagothrix*. In addition, changes in transverse process width were compared across vertebrae within species. All statistics on osteological data were two-tailed t -tests.

RESULTS

Kinematic differences

The angular values for sway are summarized in Table 1, and representative images are shown in Figure 8. Both measures of lateral sway (chest-vertical and groin-vertical) show that *Lagothrix* swings outward from the vertical much farther than *Ateles*. Lateral sway also varies with tail placement. In *Ateles*, lateral sway is lowest when the tail is on the support. No evidence was found that the side of the support the tail was gripping or which hand was in contact with the support influenced body sway. Note

also that in *Ateles*, the chest and groin deviate in opposite directions from the vertical, while in *Lagothrix*, both deviate to the same side (Fig. 8).

Osteological differences

Figure 9 shows lateral radiographs of *Ateles* and *Lagothrix*. *Ateles* has a longer tail composed of more numerous, relatively shorter elements compared to *Lagothrix*. In addition, Figure 9 demonstrates the three sections of the tail in *Ateles* and highlights the relatively long first segment of *Ateles*.

These differences were quantified, and the results are given in Table 2 and Figure 10. *Ateles* has a relatively longer tail (Fig. 10) with more numerous, relatively shorter caudal elements (Table 2) compared to *Lagothrix* ($P < 0.001$ in both comparisons). In addition, the first segment (proximal) is relatively longer and contains more numerous, relatively shorter elements in *Ateles* ($P < 0.001$). The sacro-caudal articulation angle (Figs. 7, 9, 10) in *Ateles* is

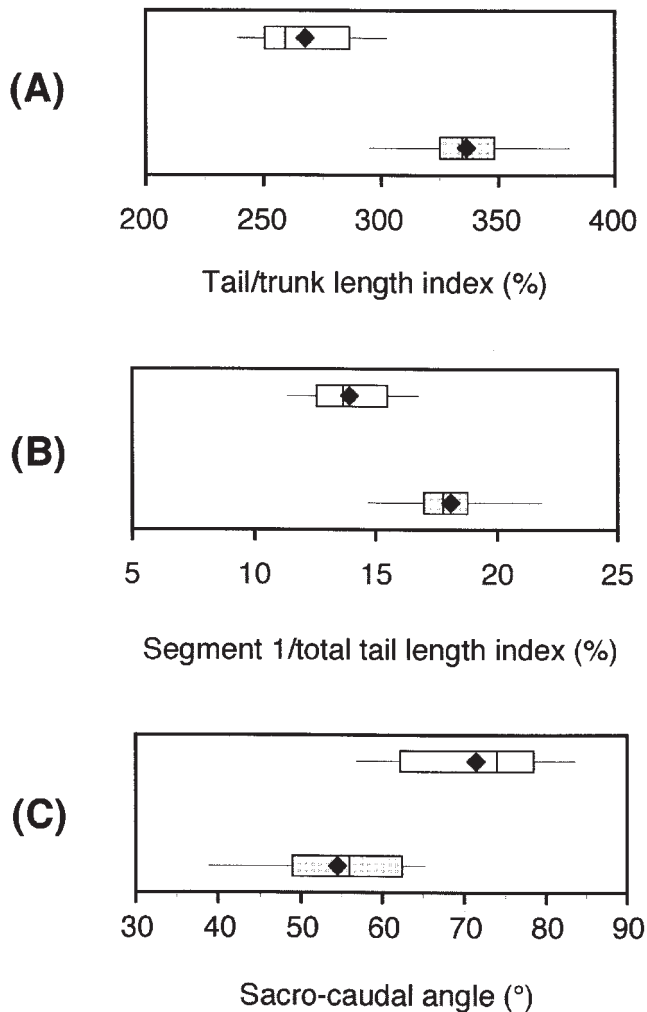


Fig. 10. Box-plot figures for values of (A) standardized tail length, (B) standardized segment 1 length, and (C) sacro-caudal angle. Shaded gray boxes show values for *Ateles*; open boxes show values for *Lagothrix*. Diamonds represent mean. Vertical lines represent median. Boxes encompass 50% of data between 25th–75th percentiles. Horizontal lines span 80% of data between 10th–90th percentiles. *Ateles* has a significantly longer tail, a longer segment 1, and a more acute sacro-caudal angle.

significantly ($P < 0.001$) more acute than it is in *Lagothrix*, thereby imparting a greater natural extension ability to the tail.

In *Ateles*, the relative width of the transverse process increases continuously from caudal 1 to caudal 5, with significant differences between caudal 2/caudal 3 ($P < 0.02$) and caudal 3/caudal 4 ($P < 0.003$) (Fig. 11). In *Lagothrix*, in contrast, there is no significant difference in relative width between the various vertebrae, and changes in width do not form a continuous pattern from caudal 1 to caudal 5 (Fig. 11). Although there is still considerable overlap of the ranges of the index, the transverse processes in *Ateles* are significantly wider than those of *Lagothrix* for caudal 4 ($P < 0.007$), caudal 5 ($P < 0.002$), and caudal 6 ($P < 0.03$) (Fig. 11).

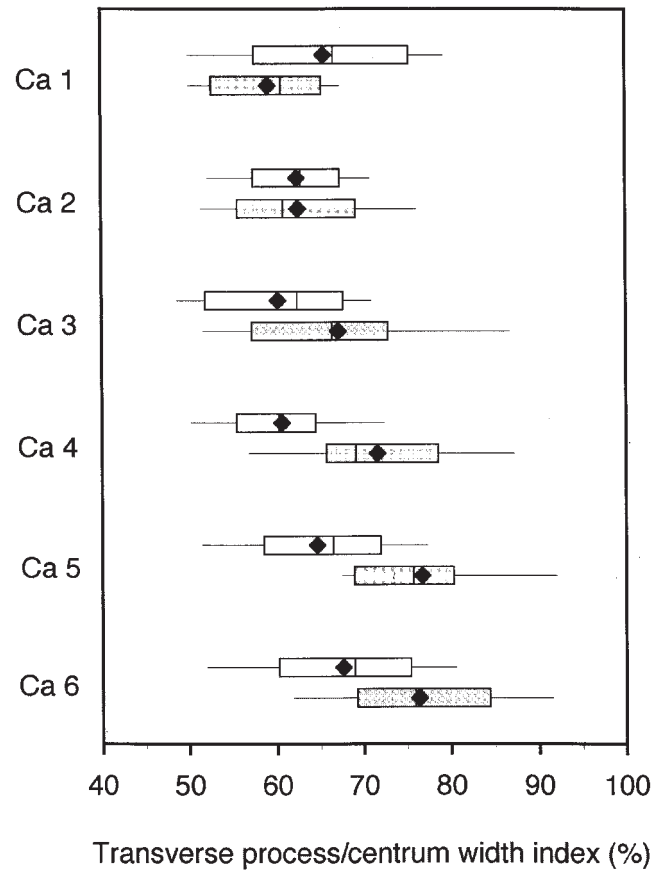


Fig. 11. Box-plot figure representing standardized width of transverse process from caudal vertebra 1 (Ca1) through caudal vertebra 6 (Ca6). *Lagothrix* is shown in open boxes; *Ateles* is in shaded boxes. Diamonds, boxes, and vertical and horizontal lines represent same parameters as in Figure 10. In this segment, *Ateles* shows progressively wider transverse processes from proximal to distal, whereas *Lagothrix* does not. For vertebrae Ca4–Ca6, *Ateles* has significantly wider transverse processes compared to *Lagothrix*.

DISCUSSION

The results of this study support the view that the prehensile tail of *Ateles* plays a more active role in the dynamics of tail-assisted brachiation than previously proposed. In contrast, the tail of *Lagothrix* appears to function more like the “fail-safe” mechanism proposed by Stern et al. (1980) and Jungers and Stern (1981). The tail of *Ateles*, as reported previously by various authors, usually grasps the support only with every other handhold, and has an extended period during which it moves freely while reaching forward to grab the support (Carpenter and Durham, 1969; Jenkins et al., 1978; Turnquist et al., 1999). This contrasts with *Lagothrix*, whose tail is either firmly grasping the support or sliding forward, barely clearing the top of the support (Turnquist et al., 1999). In *Ateles*, the long distance that the tail reaches forward to grasp a support leads to very acute hyperextended tail-body angles during tail-assisted brachiation. The difference in tail-body angle between *Ateles* and *Lagothrix* during

tail-assisted brachiation is reflected in the number and size of the caudal vertebrae and the sacro-caudal articulation. A relatively longer proximal tail segment (segment 1) with more numerous and shorter vertebrae, combined with a more acute sacro-caudal articulation, allows the tail of *Ateles* to achieve a greater degree of extension compared to *Lagothrix*.

The myological, osteological, and behavioral evidence presented in this study all lend support to the suggestion by Jenkins et al. (1978) that an important role of the prehensile tail in *Ateles* is to control lateral sway. Lemelin (1995) proposed that the presence of a large abductor caudae medialis muscle may allow *Ateles* to control lateral body sway. The expanded transverse processes noted here in *Ateles* appear to be correlated with the presence of a large abductor caudae medialis muscle. Our kinematic data clearly show reduced lateral sway of the body in *Ateles* compared to *Lagothrix*. It is worth noting that tail length alone could contribute to the observed differences in lateral body sway. If two animals swung out laterally the same linear distance, the animal with the shorter tail would have greater angular deviations than the animal with the longer tail. This suggests that tail length alone may help moderate lateral sway to some degree. However, the magnitude of the differences observed between *Ateles* and *Lagothrix* is such that tail length alone cannot account for the much smaller degree of lateral sway found in *Ateles*. Moreover, these small values found in *Ateles* (Table 1) accord with the fact that this subject remained directly below the pole during tail-assisted brachiation, with the chest deviated to one side of the pole while the groin deviated to the other (Fig. 8). Therefore, it seems likely that lateral sway in *Ateles* is mediated in larger part by the relatively large abductor caudae medialis muscle.

This conclusion is supported by the fact that lateral body sway in *Ateles* is best controlled when the tail is grasping the support. However, lateral sway in *Ateles*, even when the tail is not in use, never reaches the degree observed in *Lagothrix*. This suggests several possibilities. For example, *Ateles* may have additional mechanisms such as recruitment of shoulder musculature or hindlimb movements that may help moderate lateral sway. Alternatively, by using the tail to control lateral sway every other handhold, *Ateles* may control its side-to-side momentum in such a way that limits how far it can swing out when the tail is not in contact. Nonetheless, the fact that lateral body sway in *Ateles* doubles when the tail is off the support does indeed suggest that the tail plays an important role in controlling side-to-side motion during tail-assisted brachiation.

This study shows a clear association between musculoskeletal traits and the kinematics of the tail in *Ateles* and *Lagothrix*. Furthermore, osteological differences such as those described above can contribute to inferences about prehensile tail use in fossil atelines such as *Protopithecus* and *Caipora*

(Cartelle and Hartwig, 1996; Hartwig and Cartelle, 1996) and to understanding suspensory behavior in tailless Miocene catarrhines (Rose, 1983, 1989, 1994).

ACKNOWLEDGMENTS

This study was supported by funds from the National Science Foundation (SBR-9222526 to M.D.R. and J.E.T.), the School of Medicine of the University of Puerto Rico, the National Center for Research Resources (Research Centers in Minority Institutions RR-03051), the National Institutes of Health (to J.E.T.), and the L.S.B. Leakey Foundation (to M.D.R.). The assistance and hospitality of Dr. Sian Evans, DuMond Conservancy, is greatly appreciated, and we thank Sharon DuMond (Monkey Jungle, Miami, FL) for access to *Ateles*. We thank Mark Spencer for the drawings in Figures 3A, 5, and 7. We thank Kristin Gardner for her invaluable help in designing the method for analysis of lateral sway, data collection, and overall contributions to this project. The comments of Clark Larsen and two anonymous reviewers greatly improved the manuscript.

LITERATURE CITED

- Ankel F. 1962. Vergleichende Untersuchungen über die Skelettmorphologie des Griefschwanzes sudamerikanischer Affen. *Z Morphol Okol Tiere* 52:131–170.
- Ankel F. 1963. Zur Morphologie des Griefschwanzes bei sudamerikanischen Affen. *Z Morphol Anthropol* 53:12–18.
- Ankel F. 1972. Vertebral morphology of fossil and extant primates. In: Tuttle RH, editor. *Functional and evolutionary biology of primates*. New York: Aldine. p 223–240.
- Cant JGH. 1986. Locomotion and feeding postures of spider and howling monkeys: field study and evolutionary interpretation. *Folia Primatol (Basel)* 46:1–14.
- Cant JGH, Youlatos D, Rose MD. 2001. Locomotor behavior of *Lagothrix lagothricha* and *Ateles belzebuth* in Yasuni National Park, Ecuador: patterns and nonsuspensory modes. *J Hum Evol* 41:141–166.
- Cant JGH, Youlatos D, Rose MD. 2003. Suspensory locomotion of *Lagothrix lagothricha* and *Ateles belzebuth* in Yasuni National Park, Ecuador. *J Hum Evol* 44:685–699.
- Carpenter CR, Durham NM. 1969. A preliminary description of suspensory behavior in nonhuman primates. In: Hoffer HO, editor. *Recent advances in primatology. Proceedings of the Second International Congress of Primatology, Atlanta. Volume 2*. Basel: Karger. p 147–154.
- Cartelle C, Hartwig WC. 1996. A new extinct primate among Pleistocene megafauna of Bahia, Brazil. *Proc Natl Acad Sci USA* 93:6405–6409.
- Chang YH, Bertram JE, Ruina A. 1997. A dynamic force and moment analysis system for brachiation. *J Exp Biol* 200:3013–3020.
- Defler TR. 1999. Locomotion and posture in *Lagothrix lagothricha*. *Folia Primatol (Basel)* 70:313–327.
- Durham NM. 1975. Some ecological, distributional, and group behavioral features of Atelinae in southern Peru: with comments on interspecific relations. In: Tuttle RH, editor. *Socioecology and psychology of primates*. The Hague: Mouton Publishers. p 87–102.
- Erikson GE. 1963. Brachiation in New World monkeys and in anthropoid apes. *Symp Zool Soc Lond* 10:135–164.
- Fleagle JG. 1976. Locomotion and posture of the Malayan siamang and implications for hominoid evolution. *Folia Primatol (Basel)* 26:245–269.

- Fleagle JG, Mittermeier RA. 1980. Locomotor behavior, body size and comparative ecology of seven Surinam monkeys. *Am J Phys Anthropol* 52:301–314.
- Garber PA, Rehg JA. 1999. The ecological role of the prehensile tail in white-faced capuchins (*Cebus capucinus*). *Am J Phys Anthropol* 110:325–329.
- German RZ. 1982. The functional morphology of caudal vertebrae in New World monkeys. *Am J Phys Anthropol* 58:453–460.
- Hartwig WC, Cartelle C. 1996. A complete skeleton of the giant South American primate *Protopithecus*. *Nature* 381:307–311.
- Hunt KD, Cant JGH, Gebo DL, Rose MD, Walker SE, Youlatos D. 1996. Standardized descriptions of primate locomotor and postural modes. *Primates* 37:363–387.
- Jenkins FA Jr, Dombrowski PJ, Gordon EP. 1978. Analysis of the shoulder in brachiating spider monkeys. *Am J Phys Anthropol* 48:65–76.
- Jungers WL. 1985. Body size and scaling of limb proportions in primates. In: Jungers WL, editor. *Size and scaling in primate biology*. New York: Plenum Press. p 345–388.
- Jungers WL, Stern JT Jr. 1981. Preliminary electromyography of brachiation in gibbons and spider monkeys. *Int J Primatol* 2:19–33.
- Jungers WL, Stern JT Jr. 1984. Kinesiological aspects of brachiation in Lar gibbons. In: Preuschoft H, Chivers DJ, Brockelman WY, Creel N, editors. *The lesser apes*. Edinburgh: Edinburgh University Press. p 119–134.
- Lemelin P. 1995. Comparative and functional myology of the prehensile tail in New World monkeys. *J Morphol* 224:351–368.
- Lewis OJ. 1969. The hominoid wrist joint. *Am J Phys Anthropol* 30:251–268.
- Lewis OJ. 1971. The contrasting morphology found in the wrist joint of semibrachiating monkeys and brachiating apes. *Folia Primatol (Basel)* 16:248–256.
- Meldrum DJ. 1998. Tail-assisted hind limb suspension as a transitional behavior in the evolution of the platyrrhine prehensile tail. In: Strasser E, Fleagle J, Rosenberger A, McHenry H, editors. *Primate locomotion: recent advances*. New York: Plenum Press. p 175–200.
- Mittermeier RA. 1978. Locomotion and posture in *Ateles geoffroyi* and *Ateles paniscus*. *Folia Primatol (Basel)* 30:161–193.
- Mittermeier RA, Fleagle JG. 1976. The locomotor and postural repertoires of *Ateles geoffroyi* and *Colobus guereza* and a reevaluation of the locomotor category semibrachiation. *Am J Phys Anthropol* 45:235–256.
- Rose MD. 1983. Miocene hominoid postcranial morphology: monkey-like, ape-like, neither, or both? In: Ciochon RL, Corrucini RS, editors. *New interpretations of ape and human ancestry*. New York: Plenum Press. p 405–417.
- Rose MD. 1989. New postcranial specimens of catarrhines from the middle Miocene Chinji formation, Pakistan: descriptions and a discussion of the proximal humeral functional morphology in anthropoids. *J Hum Evol* 18:131–162.
- Rose MD. 1994. Quadrupedalism in Miocene catarrhines. *J Hum Evol* 26:387–412.
- Rosenberger AL. 1983. Tale of tails: parallelism and prehensility. *Am J Phys Anthropol* 60:103–107.
- Schultz AH. 1961. Vertebral column and thorax. In: Hofer H, Schultz AH, Starck D, editors. *Primatologia IV*. New York: Karger p 1–66.
- Sokal RR, Rohlf FJ. 1981. *Biometry*. 2nd ed. New York: W.H. Freeman and Co.
- Spencer MA, Spencer GS. 1995. Video-based three dimensional morphometrics. *Am J Phys Anthropol* 96:443–453.
- Stern JT Jr, Wells JP, Jungers WL, Vangor AK, Fleagle JG. 1980. An electromyographic study of the pectoralis major in atelines and *Hylobates*, with a special reference to the evolution of a pars clavicularis. *Am J Phys Anthropol* 52:13–25.
- Turnquist JE. 1975. The elbow and forearm of *Ateles*: an anatomical and behavioral study of locomotion. PhD. dissertation. Philadelphia: University of Pennsylvania.
- Turnquist JE, Schmitt D, Rose MD, Cant JGH. 1999. Pendular motion in the brachiation of captive *Lagothrix* and *Ateles*. *Am J Primatol* 48:263–281.
- Youlatos D. 2003. Osteological correlates of tail prehensility in carnivorans. *J Zool* 259:423–430.