Tale of Tails: Parallelism and Prehensility

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ABSTRACT   The occurrence of prehensile tails among only five platyrrhine genera—*Cebus, Alouatta, Lagothrix, Ateles,* and *Brachyteles*—might be interpreted as evidence that these are a closely related, possibly monophyletic group. In the absence of behavioral data, it is impossible to test whether all possess equivalent biological roles; such would lend credence to the idea that their tails evolved from an homologous, derived character complex. Contrariwise, the tendency for species of *Cebus* to have "averagely" proportioned or relatively short tails, in contrast to the relatively elongate tails of howlers and other atelines; osteological differences in caudal and sacral morphology; and a lack of ateline-like tail/neocortex correlates in *Cebus,* all imply that prehensility has evolved twice in parallel: once (homologously) in atelines and again in capuchins.

Despite the vague claims of yesterday's texts and taxonomies, which often stated or implied that the tails of the nonclawed New World monkeys are "nearly always of considerable length and frequently prehensile" (Dollman, 1933), we now know that the grasping tail is limited to a handful of genera. Only in *Cebus, Alouatta, Lagothrix, Ateles,* and *Brachyteles* are tails capable of a finger-like clasping that one could call "prehension." This excludes several other candidates, like *Saimiri* and *Callicebus,* which commonly engage their tails in behaviors such as body wrapping or tail twinning, respectively, but apparently without the degree of coordination—and certainly sensation—manifest in the ateline forms. (Following Rosenberger (1981), ceboids are reclassified into Families Cebidae, including Cebinae and Callitrichinae, and Atelidae, with Pitheciinae and Atelinae, including *Alouatta.*) Although some modern authors have consistently distinguished the tail of *Cebus* from that of atelines on account of the latter's ventral skin-covered sensory pad, occasionally labeling the capuchin condition "semiprehensile" and the ateline pattern ("fully") "prehensile" (e.g., Napier, 1976; Hershkovitz, 1977), we still lack a comprehensive behavioral study of tail use in any of these taxa. Thus the evidence does not justify the frequent claim that apart from contrastive tactile abilities all five

genera present tails that are functionally and equally prehensile. There also seems to be some confusion in the literature concerning the degree of morphological similarity shared by *Cebus* and atelines, especially regarding functionally relevant features such as relative tail length. Ankel (1972), for example, emphasized that both ateline and capuchin tails are long, whereas Napier (1976) distinguished *Cebus* monkeys on account of their relatively short tails. Inferential inconsistencies and clear-cut anatomical differences notwithstanding, the restricted taxonomic distribution of semi- and fully prehensile tails among the platyrrhines poses one of the classic problems in New World monkey systematics (Rosenberger, 1981). Of course, tail prehensility must be a derived characteristic among primates, and it seems that many early workers drew the obvious conclusion that this demonstrated a close relationship between *Cebus* and the Atelinae. Although other interpretations of *Cebus* affinities (e.g., Simpson, 1945; Hill, 1960; Rosenberger, 1979) cast doubt upon such a conclusion, the issue has not been adequately resolved on morphological grounds, and it continues to erroneously influence scenarios of platyrrhine evolution (e.g., Hershkovitz, 1977),

even when couched in gradistic terms (Rosen-berger, 1980). The purpose of this brief note is to bring together some observations that suggest that the grasping abilities of the tails of *Cebus* and the atelines have evolved independently and in parallel. I attempt to demonstrate this by showing that significant morphological differences exist and combine to form two different patterns of organization, one in *Cebus* and the other shared in common by *Alouatta, Lagotrhix, Ateles*, and *Brachyteles*. Like all arguments designed to refute hypotheses of shared homology, this one is largely negative and, when taken alone, far from foolproof. However, in conjunction with positive evidence on the phylogenetic relationships among the animals in question (e.g., Rosenberger, 1979), it seems to be the most reasonable and robust interpretation of many homologous character distributions and numerous contrasting morphologies.

To my knowledge, Ankel's (e.g., 1972) work represents the most complete discussion of the osseous anatomy of platyrrhine tails. She distinguished the ateline caudal region by a number of features: eight proximal elements, each of which is relatively short and bears lumbar-like articulations and elevated neural arches; a distally positioned longest-tail vertebra; short and flattened terminal elements; differentially enlarged, and rearranged, dorsal and ventral muscle masses. Together with a relative increase in the size of the sacral canal and the external tactile pad, these traits are thought to enhance the flexibility, proximal articular integrity, power, and nervous coordination of the tail. Ankel (see also German, 1981) stated and implied that the *Cebus* morphology is nearer that of atelines, and "intermediate" relative to the nonprehensile tails of other platyrrhines in almost all ways. Still, she pointed to the following discrete characters as non-ateline: six proximal elements, all with standard caudal zygopophyses and without evidence of an abbreviated length; and absence of flattened terminal elements. Additionally, the index of sacral canal size is lower in *Cebus* (see below) and the appendage lacks a friction skin. Thus, added to the well-known hirsute versus glabrous difference are osseous features that probably relate to caudal dexterity, curling potential, and articular strength—i.e., a combination of continuous and discrete features of probable functional and behavioral significance. It seems reasonable to presume that these involve both acrobatic and strictly tactile biological roles.

There is also some evidence that the relative external length of ateline tails is generally quite long and includes a comparatively large number of caudal vertebrae, whereas that of *Cebus* is reduced in both respects. In a bivariate plot (Fig. 1) of log head and body length versus external tail length for a spectrum of platyrrhines, the cluster of capuchin species tends to exhibit tails that are of average or short length by comparison with ceboids of roughly similar body size or of the entire array. This appears to contrast the proportions of atelines—especially *Lagothrix, Ateles*, and *Brachyteles*. These data are applied to a number of models of interspecific scaling to corroborate this observation, although I emphasize that such manipulations can support only the most general conclusions. Using logarithmic regressions of sex-pooled means for 26 platyrrhine species, specified in Figure 1, I have generated predicted lengths for capuchin and ateline tails. For species of *Cebus*, the observed mean lengths tend to be somewhat less than the predicted values, whereas the converse is true of atelines, particularly *Ateles, Brachyteles*, and *Lagothrix*, by a wide margin.

For all the included taxa, the pattern and magnitude of deviations from the least-squares regression lines are consistent across five of the six models (Table 1), whether devised or along taxonomic lines to reflect phylogeny or upon functional criteria to eliminate biases that might arise when comparing forms having widely divergent caudal adaptations. Two additional models, based exclusively on 1) atelids and 2) nonprehensile-tailed cebids plus atelids, are not shown because their low correlation coefficients (0.15; −0.06) would make similar inferences moot at best. Those regression models with the highest correlation coefficients, models II, III, and IV, which avoid the necessity of accounting for the great variance encountered among the heterogeneous atelines, are of particular interest. Models II and IV suggest that by comparison with unspecialized cebids or ceboids, for an animal of its "size"—i.e., head-and-body length—*Cebus* has a tail of "average" or expected length. Model IV, which provides a specifically cebid phylogenetic standard of interspecific allometry, emphatically indicates that *Cebus* tails are relatively shorter than any of its presumed closest relatives (e.g., Rosenberger, 1979, 1981). This same regression framework also gives the impression of atelines having normally proportioned or even reduced (e.g., *Alouatta*) tails. However, the discrepancy be-
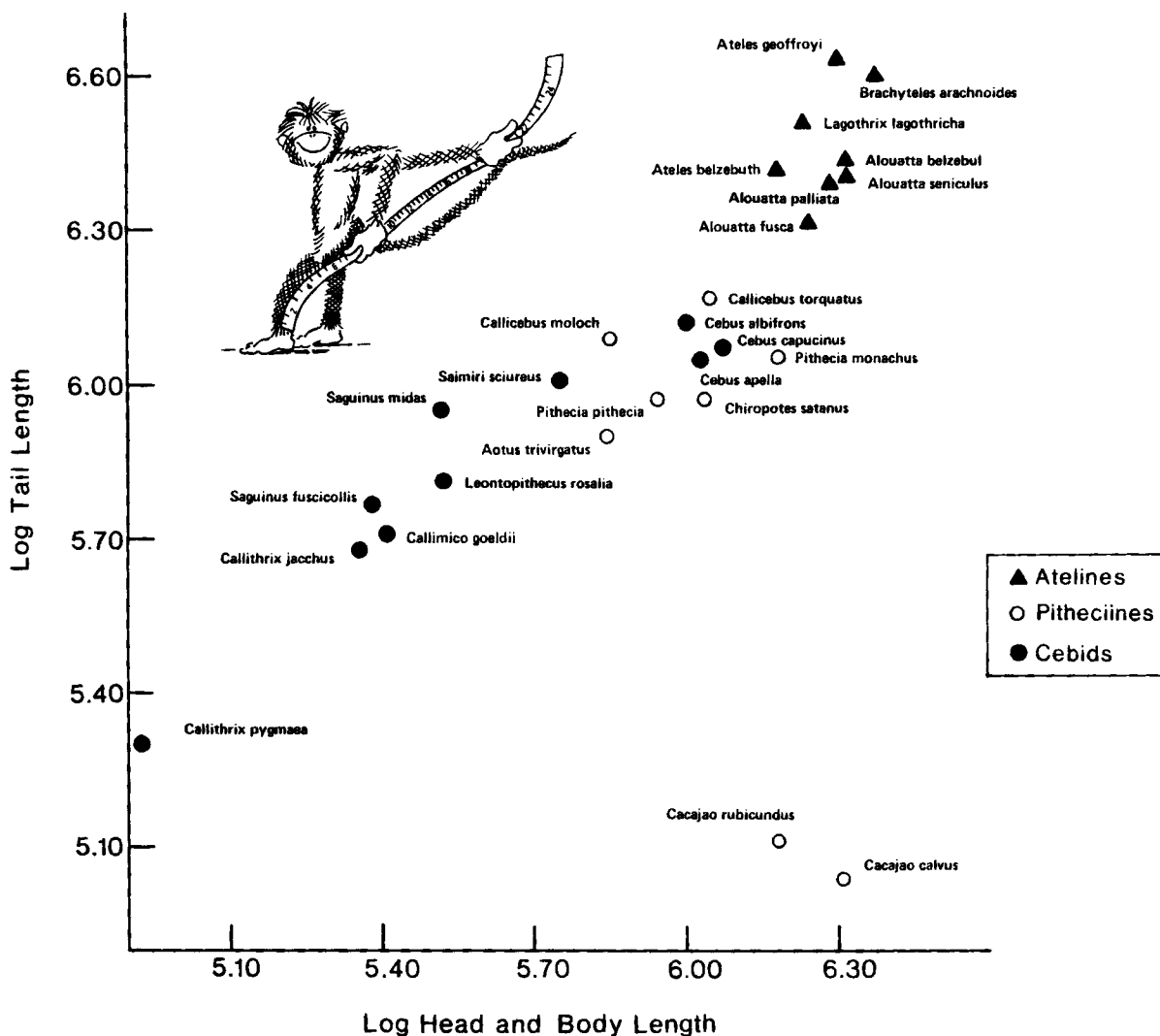
Fig. 1. Scatter diagram showing the relationship between adult head and body length, a measure of body size, and external tail length in a sample including all living ceboid genera. Points represent sex-pooled species means. See Table 1 for data sources, regression models, parameters, and relative measures of tail length based upon regression predictions. The visual impression that the *Cebus* species have "averagely" proportioned or relatively short tails, in contrast to the atelines, is confirmed for both functional and phyletic subsamples.

tween the predictions generated by model IV versus all others is so great in this particular cross-phyletic comparison, which also involves a huge body size disjunction essentially lacking any range overlap, that the extrapolation to atelines has dubious value if it is at all justifiable. All in all, it appears that atelines do have relatively long tails, although it is least elongate in *Alouatta*. Finally, to stretch this approach to its limits, extrapolating a logarithmic regression of head and body length versus average number of caudal vertebrae in nonspecialized platyrrhine genera (*Callithrix, Callimico, Saimiri, Callicebus, Pithecia, Aotus;* data from Schultz (1961); $r=0.63$, exp.$=-0.115$, int.$=3.91$), in analogy to model

TABLE 1. Ratio between observed mean length and predicted tail length for semiprehensile and prehensile-tailed adult ceboids, sex-pooled[1]

Species	Models					
	I	II	III	IV	V	VI
Cebus capucinus	0.98	0.95		0.77	0.99	0.87
Cebus albifrons	1.07	1.04		0.85	1.07	0.92
Cebus apella	0.98	0.95		0.78	0.98	0.85
Alouatta belzebul	1.22	1.18	1.13	0.89	1.25	
Alouatta fusca	1.13	1.09	1.05	0.84	1.15	
Alouatta seniculus	1.19	1.14	1.10	0.86	1.22	
Alouatta palliata	1.19	1.14	1.10	0.86	1.21	
Ateles belzebuth	1.30	1.25	1.21	0.98	1.32	1.22
Ateles geoffroyi	1.43	1.45	1.40	1.10	1.51	1.51
Brachyteles arachnoides	1.40	1.35	1.29	1.00	1.45	1.45
Lagothrix lagothricha	1.38	1.33	1.29	1.03	1.33	1.33

[1]Model I—All ceboids. N = 26; int = 2.66; exp = 0.57; r = 0.51.
Model II—Unspecialized ceboids (excludes atelines, Cebus, Cacajao). N = 13; int = 2.46; exp = 0.60; r = 0.92.
Model III— All cebids. N = 10; int = 2.26; exp = 0.64; r = 0.95.
Model IV—Unspecialized cebids (excludes Cebus). N = 7; int = 0.93; exp = 0.89; r = 0.97.
Model V—Unspecialized atelids (excludes atelines, Cacajao). N = 6; int = 3.05; exp = 0.50; r = 0.59.
Model VI—Unspecialized atelids plus Alouatta. N = 10; int = 5.86; exp = 0.06; r = 0.56.
Data from Kellogg and Goldman, 1944; Napier, 1976; Hershkovitz, 1977; Rosenberger, pers. obs.

II, similarly overestimates the count for Cebus (observed/expected = 0.95) but underestimates the values for Alouatta (1.12), Lagothrix (1.08), and Ateles (1.28). Thus the same contrast between Cebus and atelines obtains when the number of caudal segments is considered.

In spite of the limitations of the data used in this examination, it does seem that, on the whole, the tail of Cebus is not relatively long, and may be slightly short for a platyrrhine or cebid of its linear dimensions, confirming Napier's (1976) observation. In contrast, the tail of Alouatta is at least moderately elongate, and those of Lagotrhix, Ateles, and Brachyteles are relatively very long. Thus the evidence of tail proportions argues against the notion that the semiprehensile tail of Cebus is intermediate, phyletically and functionally, between ateline and nonateline platyrrhines. Moreover, these data imply that in at least some species of Cebus tails are perhaps autapomorphically reduced in length (assuming that Cacajao is monophyletically related elsewhere, which seems doubtless true). Furthermore, the anomalously short capuchin tail may partially account for its rather low rank on Ankel's (1972) scale of sacral canal indices: its value of 80.7 is hardly "intermediate" between that of Saimiri (77.1) and atelines (99.4–121.0). The low index is perhaps better explained as a correlate of tail shortening (and/or lesser body size?) rather than by an implicit appeal to the absence of an ateline-like hyperinnervation and vascularization of the caudal region, which again alleges intermediacy between nonspecialized and fully prehensile tails.

Morphological and neurological studies of platyrrhine brains and endocasts supply still another basis for evaluating the evolution of prehensile tails, and lend support to the propositions developed here. Cortical mapping studies reviewed by Radinsky (1972) have shown that, in Ateles, caudal sensorimotor representation has shifted from its primitive position within the great sagittal sulcus to a more lateral location on the dorsolateral surface of the brain. Following this work, Radinsky suggested that several topographic features of the sulcul pattern of Ateles, such as the confluence of the Sylvian and the intraparietal sulci, which are also clearly shown in Brachyteles and Lagothrix (e.g., Falk, 1981), are correlated with this shift and expansion. A similar condition occasionally seen in Saimiri is demonstrably not functionally related to homologous expansion of the tail's sensorimotor area (see Falk, 1981). It is noteworthy that the poorly folded Alouatta brain, which is quite small relative to its body size (e.g., Gould, 1975), nonetheless shares this as well as other cortical features that are uniquely derived and possibly related to tail prehensility with other members of the Atelinae (see Hershkovitz, 1970; Falk, 1981). Thus the prehensile complex common to all atelines may be seen to extend consistently from the osteology and integument of the tail itself to its neurological manifestation. The important point here is that in the relatively enlarged

(e.g., Clutton-Brock and Harvey, 1980) and elaborate brain of *Cebus*, there is no confluence of Sylvian and intraparietal fissures; even in *Alouatta*, where the cortex is poorly folded, the converse is true.

In conclusion, it appears that *Cebus* differs from *Alouatta*, *Lagothrix*, *Ateles*, and *Brachyteles* in a host of features relating to the morphology of the tail, its proportions, and cortical correlates. This implies that the semiprehensile faculties of *Cebus* are not homologous, and may have evolved independently from that of atelines. The confirmation of this hypothesis requires another data set and the demonstration that *Cebus* is phyletically related to a separate clade; the evidence strongly favors a sister-group relationship between *Cebus* and *Saimiri* (e.g., Rosenberger, 1979). In terms of relative tail length, which marks a shared specialization of the ateline tail complex, *Cebus* may have evolved in the opposite direction, toward autapomorphic abbreviation. The latter point, in particular, diminishes the argument against parallelism—i.e., that the tail complex of *Cebus* is merely at a more primitive "stage" than an ateline such as *Alouatta*—because howlers share with the other atelines all of the other morphological peculiarities of prehensility even without being comparably elongate. One would thus be forced to argue that *Cebus* presages atelines behaviorally but not morphologically—a patently unacceptable line of phyletic reasoning. It is hoped that studies of tail use in locomotor contexts will clarify more aspects of this problem and explain why platyrrhines may be preadapted to the parallel evolution of prehensility, as I have elsewhere suggested (Rosenberger, 1977). Nevertheless, now that the question of nonhomology has been specifically addressed, amplifying the concern of many twentieth-century systematists (Rosenberger, 1981), it behooves us to consider once again the evidence of *Cebus* affinities and the rationale for taxonomically separating *Alouatta* from the other "fully" prehensile-tailed monkeys.

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