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## TROPICAL FOREST STRUCTURE AND THE DISTRIBUTION OF GLIDING AND PREHENSILE-TAILED VERTEBRATES

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Tropical forest vertebrates with similar ecological roles on different continents often have remarkably convergent morphology (Dubost 1968). One striking difference between the tropical forest faunas of Asia, Africa, and America is in the number of vertebrates in each that have evolved the specialized locomotory adaptations of gliding membranes or prehensile tails. Most gliding vertebrates are found in the Asian tropics, most with prehensile tails in the Neotropics, and few of either in Africa (table 1).

Although this difference could be a historical accident, the constancy of these differences across taxonomic lines suggests that they may have resulted from different selective pressures on arboreal vertebrates in each region. The most likely source of such pressures would be in differences in the structure of the forest canopy in which the animals travel and feed. While the overlapping tree crowns of the tropical forest canopy give an illusion of a continuously connected, undulating surface when seen from above, from the arboreal vertebrate viewpoint that canopy consists largely of open space through which lianas offer the only structural continuity over any appreciable distance (Grand 1983). Except for large trees, intercontinental comparisons of tropical forest composition and structure are nonexistent. Here we present data that demonstrate what appear to be significant differences in the forest structure of the three tropical regions and suggest that these are correlated with the regional differences in locomotory adaptations.

A prehensile tail is one which can support alone the weight of the suspended body; semiprehensile tails can be wrapped around branches and support a significant part, but not all, of the body weight. In animals like howler and spider monkeys, the prehensile tail weighs as much as one of the hindlimbs, a significant anatomical investment in musculature and neuromuscular reorganization that suggests considerable adaptive value (Grand 1983). Prehensile tails have evolved independently in two suborders of reptiles, an order of amphibians, and six orders of mammals, which cover a broad ecological range. Although prehensile tails have different functions in different taxa, in general they are used for either support or

TABLE I  
A. FAMILIES AND GENERA OF GLIDING VERTEBRATES  
(Nos. of species in parentheses)

Western Amazonia	Borneo	Gabon
<i>Mammalia</i>		
none	Cynocephalidae	Anomaluridae
	<i>Cynocephalus</i> (1)	<i>Anomalurus</i> (1)
	Sciuridae	<i>Anomalurops</i> (1)
	<i>Petaurillus</i> (2)	<i>Idiurus</i> (1)
	<i>Iomys</i> (1)	
	<i>Aeromys</i> (2)	
	<i>Petinomys</i> (4)	
	<i>Hylapetes</i> (2)	
	<i>Pteromyscus</i> (1)	
	<i>Petaurista</i> (2)	
<i>Amphibia</i>		
none	Rhacophoridae†	none
	<i>Rhacophorus</i> (3)	
<i>Reptilia</i>		
none	Gekkonidae	none
	<i>Ptychozoon</i> (3)	
	<i>Cosymbotus</i> (2)	
	Agamidae†	
	<i>Draco</i> (8)	
	Colubridae	
	<i>Chrysopelia</i> (2)	
Total species . . . . .	(0)	(33)

B. FAMILIES AND GENERA OF PREHENSILE-TAILED VERTEBRATES

Western Amazonia	Borneo	Gabon
<i>Mammalia</i>		
Didelphidae	Manidae	Manidae
<i>Didelphis</i> (1)	<i>Manis</i> (1)	<i>Manis</i> (2)
<i>Caluromys</i> (1)	Viverridae	Muridae
<i>Caluromysiops</i> (1)	<i>Arctictis</i> (1)	<i>Dendromus</i> (1)
<i>Monodelphis</i> (2)		
<i>Philander</i> (2)		
<i>Marmosa</i> (3)		
<i>Metachirus</i> (1)		
<i>Glironia</i> (2)		
Cebidae		
<i>Ateles</i> (1)		
<i>Lagothrix</i> (2)		
<i>Alouatta</i> (1)		
<i>Cebus*</i> (2)		
Myrmecophagidae		
<i>Tamandua</i> (1)		
<i>Cyclopes</i> (1)		
Erethizontidae		
<i>Coendou</i> (1)		
Pracyonidae		
<i>Potos</i> (1)		
<i>Nasua*</i> (1)		

(Continued)

TABLE I (Continued)

## B. FAMILIES AND GENERA OF PREHENSILE-TAILED VERTEBRATES

Western Amazonia		Borneo		Gabon
<i>Amphibia</i>				
Plethodontidae†		none		none
<i>Bolitoglossa</i>	(5)			
<i>Reptilia</i>				
Viperidae		Viperidae†		Viperidae
<i>Bothrops</i>	(3)	<i>Trimuresurus</i>	(3)	<i>Atheris</i>
Boidae		Boidae†		Boidae
<i>Boa</i>	(1)	<i>Python</i>	(1)	<i>Python</i>
<i>Corallus</i>	(3)	Colubridae†		Chamaeleonidae
<i>Epicrates</i>	(1)	<i>Boiga</i>	(1)	<i>Chamaeleo</i>
<i>Eunectes</i>	(1)	<i>Haplopeltura</i>	(1)	
		<i>Psammodynastes</i>	(1)	
Total species . . . . .	(38)		(9)	(8)

NOTE.—We have restricted our lists to the comparable equatorial forests of western Amazonia, Borneo, and Gabon for which we have vegetation samples. Gliding has also evolved in one group of Central American frogs and prehensile tails in one Malaysian and two New Guinean genera of mice.

\* Species with semi-prehensile tails.

† Data from R. Inger who also notes 14 other species of Bornean snakes with what he considers semiprehensile tails.

‡ Data from D. Wake.

locomotion. The selective effects, if any, of vegetation structure on the evolution of prehensile tails might be expected to differ between those taxa which use them for locomotion and those in which they serve chiefly for support. The prehensile tails of arboreal frugivores, folivores, and omnivores such as opossums, monkeys, kinkajous, and porcupines are used both for support while the animals feed on branch tips or inaccessible locations and as an aid in locomotion, particularly on unstable supports and while descending (Grand 1978; Charles-Dominique et al. 1981; LHE, personal observation). For example, Grand (1983) shows that the prehensile tails of cebids confer both feeding and locomotory advantages, especially when negotiating slender branch tips that are bent by the animal's body weight. For travel along more stable supports, such as large liana stems, a prehensile tail offers little biomechanical advantage (T. Grand, personal communication).

In contrast, the prehensile tails of snakes serve a different function and are used more for support than locomotion; they are commonly found in heavy-bodied genera that use them as anchors while the rest of the body is thrown out to encircle or strike at prey. The prehensile tails of arboreal ant-feeders also have a nonlocomotory function, primarily providing a solid posterior support so that both forelegs are freed to rip apart insect nests; pangolins and tamanduas, at least, do most of their traveling and much feeding on the ground (personal observation). The chameleons and prehensile-tailed mouse in Gabon frequent thin-stemmed vegetation near the ground. Consequently, none of the few prehensile-tailed

vertebrates in Gabon (table 1) use their tails for traveling across the canopy, while most of the Neotropical genera (and perhaps Asian *Arctictis*) do. Vegetation structure should thus influence the usefulness of prehensile tails for arboreal frugivores, folivores, and omnivores, but may be less important for secondary consumers (anteaters and reptiles). With the possible exception of *Arctictis*, use of prehensile tails to move through the canopy seems restricted to the Neotropics.

Gliding requires complex morphological specialization, and it occurs in only three orders of mammals, one of reptiles, and one of amphibians. All mammalian gliders are nocturnal and all large species are folivores. Smaller species are frugivore-insectivores (Muul and Lim 1978; LHE, personal observation). Gliding is, therefore, more ecologically and taxonomically restricted than are prehensile tails. It is an adaptation of arboreal animals for energetically cheap, rapid transit between trees. Gliding may also help animals escape from predators by dropping from the canopy without injury, although some animals do this without the benefit of parachuting membranes (LHE, personal observation). Such aspects of canopy structure as differential availability of pathways for inter-tree movement would seem likely to influence the usefulness of gliding. Curiously, gliding is widespread in the Asian tropics but in Africa occurs only in one small family of rodents and in the Neotropics only in one group of Central American frogs.

Tropical forests are widely thought to be structurally similar throughout the world (Richards 1952; Leigh 1975). If the evolution of prehensile tails and gliding membranes has been influenced by canopy structure, what differences are there between African, Asian, and South American forests that could account for the different locomotory adaptations of their faunas?

During the past 9 years, one of us (AHG) has accumulated vegetational samples of 28 lowland tropical forest communities throughout the world. A standard technique was developed to sample all plants  $\geq 2.5$  cm diameter in 1,000 m<sup>2</sup> plots (Gentry 1981, 1982*b*). Relevant data include 18 samples in South and Central America, four in Africa, and two in Borneo. Analysis of the data shows the following pertinent results (table 2). (1) Total stem densities, though somewhat variable from site to site on each continent, show a similar range of variation worldwide; difference in the number of vertical supports is thus an unlikely selective factor. (2) Within the Neotropics, liana densities are quite constant; however, the African forests sampled had more lianas, and Bornean forests fewer, than did Neotropical forests (premontane and montane forests in both Africa and South America have fewer lianas than lowland sites and have been excluded from our data set). (3) There are significantly more tree-sized palms in South American forests than in the other regions.

The generalization that tropical rain forests throughout the world are structurally very similar (e.g., Richards 1952; Leigh 1975) is based on data from biomass and productivity, leaf size and shape, canopy height and degree of stratification, and tree density (Dawkins 1959; Leigh 1975). One important structural component of tropical forests which has been little studied and never compared on an intercontinental basis is lianas. The data summarized in table 2 show that, unlike tree density, liana density differs significantly between tropical America ( $\bar{x} = 71$

$\pm 21$ ), Africa ( $\bar{x} = 92 \pm 15$ ), and Asia ( $\bar{x} = 42 \pm 16$ ). America has more lianas than Asia ( $t = 1.84, p < .05$ ) and fewer than Africa ( $t = 1.81, p < .05$ ).

Although it is apparent that lianas are important in tropical forest ecosystems, their role in vertebrate ecology is only beginning to be realized (Montgomery and Sunquist 1978; Gentry 1982a). In general, their use by animals tends to parallel their frequency. For example, it is noteworthy that in Gabon the percentage of lianas used as a food source by two different primate genera is identical to the percentage that lianas contribute to total canopy foliar production in the same forest (36%, Hladik 1974). An index of the relative use of lianas by forest mammals on different continents can be deduced from their relative importance as food plants (table 3). Primates consistently use more lianas for food in Africa than in other regions.

Another important function of lianas, which often interconnect tree crowns, is to provide arboreal pathways for canopy vertebrates (e.g., Charles-Dominique 1971; Charles-Dominique et al. 1981). Suspensory postures utilizing prehensile tails are primarily adapted to cope with the downward deformation that slender branch tips undergo when burdened with the weight of an animal; they have much less biomechanical significance in inter-tree or inter-branch movement via lianas that allow the animal to bypass droop-prone branch terminals (Grand, personal communication). We believe that the presence of more lianas stretching between trees in African forests may have reduced the usefulness of specialized locomotor adaptations among African arboreal animals. Prehensile tails in Neotropical vertebrates and gliding (and brachiation) in Asian ones may help animals to cross canopy gaps that in Africa are bridged by lianas.

Another striking difference between Neotropical and Paleotropical forests is the prevalence of large palms in mature forest (table 2). Palms are an important structural feature of Neotropical forests (Moore 1973; table 2), and are known to be poorly represented in Africa (Richards 1973; Raven and Axelrod 1974) where they occur mostly outside the tropical forest in swamps and savannahs (Moore 1973; personal observation). Although there are as many palm species in Australasia as in the Americas (Corner 1966; Richards 1973), palms, except climbing rattans and some understory taxa, are much more poorly represented in Asian climax forests.

Palms may provide a difficult substrate for climbing. An unusual feature of palms which is potentially relevant from the viewpoint of vertebrate locomotion is that they seem to have mechanisms to avoid invasion by lianas (Putz 1980) and are often surrounded by gaps in the vegetation, resulting in a more discontinuous canopy. Palm leaves are often used to gain access to palm fruits and as pathways through the forest by arboreal animals, including the prehensile-tailed monkeys (Thorington, personal communication; LHE, personal observation). Palm leaves are a slippery and highly unstable substrate on which the prehensile tail is sometimes used for additional support. Frequent climbing in palm trees may have contributed to the selective advantage of prehensile tails in the Neotropics.

Finally, we have observed a third, less obvious difference between Neotropical and Paleotropical forests. Whereas in Central and South America small lianas

TABLE 2  
COMPOSITION AND STRUCTURE OF 1,000 m<sup>2</sup> SAMPLES OF LOWLAND TROPICAL FORESTS

Site	No. of Individuals ≥ 2.5 cm Diam.	No. Lianas ≥ 2.5 cm Diam.	No. Trees ≥ 10 cm Diam. (+ Lianas)	No. Palms (No. Palm spp.)	No. Palms ≥ 10 cm Diam.
<b>Neotropical</b>					
Boca de Uchire, Venezuela*	259	75	31	...	...
Calabozo, Venezuela*†	326	56	44	...	...
Blohm Ranch, Venezuela*	306	71	86(+2)	18(1)	18
Guanacaste (upland), Costa Rica*†	437	81	34	...	...
Guanacaste (gallery), Costa Rica*†	195	24	33	3(1)	...
Jauneche, Ecuador	435	123	63(+1)	3(3)	3
Madden Forest, Panama	324	76	38(+1)	14(5)	7
Rio Palenque (no. 1), Ecuador	305	63	42(+2)	47(6)	10
Rio Palenque (no. 2), Ecuador	324	45	52	59(6)	9
Pipeline Road, Panama	393	67	60(+1)	74(11)	10
Tutunendo, Colombia	523	72	81(+1)	57(15)	13
Mishana (white sand), Peru	406	59	59(+1)	10(2)	2
Mishana (lowland), Peru	483	86	83(+1)	40(9)	9
Mishana (tahuampa), Peru	514	99	70(+14)	7(3)	1
Cochacashu, Peru	359	79	77(+2)	20(4)	10
Yanomono, Peru	303	60	55(+2)	7(6)	2
Tambopata, Peru	360	82	58(+3)	28(7)	17
Los Tuxtlas, Mexico†	326	54	51(+4)	113(4)	0

Average .....	365.5	71	56.5	36.88/30.5 <sup>§</sup>	7.28/7.8 <sup>¶</sup>
<b>Africa</b>					
Makokou (no. 1), Gabon .....	339	103	51(+14)	...	...
Makokou (no. 2), Gabon .....	326	82	41(+4)	...	...
Omo Forest, Nigeria .....	331	76	85	...	...
Oban Forest, Nigeria <sup>†</sup> .....	420	105	60(+5)	10(2)	5
Average .....	354	91.5	59	2.5	1
<b>Asia</b>					
Semengoh Forest, Sarawak .....	521	26	93(+2)	...	...
Bako Forest, Sarawak .....	373	58	68(+3)	2(2)	...
Average .....	447	42	80.5	1	...

NOTE.—All sites are below 500 m altitude. Data from Gentry 1981, 1982*b*, and in prep. Two sites with relatively immature forest are excluded from the data set of Gentry 1982*b*.

\* Dry forest sites.

† Extrapolated from sample smaller than 1,000 m<sup>2</sup>

‡ Subtropical site.

§ Average without dry forest sites.

¶ Average without dry forest sites and subtropical site.

TABLE 3  
 PERCENTAGE OF IDENTIFIED PLANT FOOD SPECIES MADE UP OF LIANAS AND CLIMBERS

Species	Location	No. Plant spp. Identified in Diet	% Lianas	Reference
<b>Neotropics</b>				
Primates, 5 spp.	Manu Park, Peru	155	17	J. Terborgh, C. Janson, personal communication
<i>Aotus trivirgatus</i>	Manu Park, Peru	47	17	P. Wright, personal communication
<i>Callicebus moloch</i>	Manu Park, Peru	65	23	P. Wright, personal communication
<i>Alouatta palliata</i>	Guanacaste, Costa Rica	382	13	Glander 1978
Primates, 5 spp.	B.C.I., Panama	78	5	Hladik and Hladik 1969
<b>Asia</b>				
<i>Pongo pygmaeus</i>	Sumatra	118	20	Rijksen 1978
<i>Hylobates syndactylus</i>	Krau Reserve, Malaya	139	15	Curtin and Chivers 1978
<i>Presbytis obscura</i>	Hua Kha Keng, Thailand	31*	6	Eudey 1980
<i>Macaca</i> spp.				
<b>Africa</b>				
<i>Cercopithecus</i> , 3 spp.	Makokou, Gabon	74	35	Gautier-Hion 1980; Gautier-Hion et al. 1981
<i>Pan troglodytes</i>	Makokou, Gabon	167	31	Hladik 1973
<i>Cercopithecus mitis</i>	Lake Kivu, Zaire	34	32	Schlichte 1978
<i>Colobus satanus</i>	Douala-Edea Reserve, Cameroons	85	34	McKey 1978
<i>Loxodonta africana</i>	Bia Park, Ghana	138	43	Short 1981

NOTE.—Only data for tropical lowland sites are included; premontane forests on all continents appear to have fewer lianas and are therefore not comparable (e.g., Kibale Forest, Uganda).

\* Erroneous spellings of plant names abundant in the zoological literature. Usually we have been able to guess the correct name but one genus, none of whose likely permutations could be located in a botanical dictionary, had to be omitted from this data set.

(ca. 2.5 cm diameter) can usually be collected by simply pulling them down from the canopy, in Africa they are more firmly attached and rarely can be sampled by this method. Sometimes lianas in the Neotropics break when pulled on, especially in such families as Apocynaceae, Vitaceae, and Menispermaceae; this never happened in either Paleotropical region, even in the same families. In general, the vegetation seems more fragile in the Neotropics than in the lowland Paleotropics. Almost half of the plants eaten by elephants in an African forest were lianas (Short 1981, table 3) and we suspect that browsing by elephants that pull down terminal branches and lianas may have selected for more resistant stems and branches in African forests. We have no comparable observations for Asia, where elephants should also have influenced the vegetation. More fragile branches would make the extra hold of a prehensile tail more important in moving through a Neotropical canopy. In this context, it may be relevant that among the Cebidae, prehensile tails are found in all of the heaviest genera, semiprehensile tails in a medium-weight genus, and nonprehensile tails in lightweight genera.

It is obvious that the available data set incompletely reflects overall intracontinental variation in forest structure, especially in Asia. The neotropical sites, which range from rich soil Central American and Andean foothill locations to the extremely poor soils of lowland Amazonia and span the precipitation spectrum from 1,200 mm to ca. 9,000 mm of annual rainfall, show a greater range of variation in both liana and palm density than do the less comprehensive palaeotropical samples. In the Neotropics, lianas tend to be less frequent in the sites with unusually poor (Mishana white sand "campinarana") or unusually rich (Rio Palenque) soils, and palms are more frequent in areas that are wetter or have richer soils. Vegetation is more sclerophyllous and branches less fragile on poor soil sites on all continents. As our Asian data are all from intrinsically poor-soil Borneo, might Asian forests on richer soils be sufficiently richer in lianas and palms to obviate our structural generalizations? We believe that the continental differences suggested by the data of table 2 are valid since (1) the African sites, with their very high liana densities, are on poor soils which would have been expected to be relatively poor in lianas on the basis of the Neotropical trends. (2) Although the Bornean sites do not sample the rich soil forest found in some other parts of Southeast Asia, they can be individually matched with most-similar Neotropical sites. The Bako Park site, on very poor sandstone-derived soil, is most similar edaphically to the Mishana white sand site in Peruvian Amazonia and has exactly the same liana density but fewer palms. The Semengoh Forest site, more representative of typical mixed dipterocarp forest, is most similar edaphically to the Yanomono, Peru, lateritic soil site but has very many fewer lianas (and fewer palms) than either the Peruvian site or the even poorer-soil Bako site. There is thus no reason to expect more lianas on richer soils in Southeast Asia, and the generally low liana density suggested by our sample seems typical of mixed dipterocarp forests. (3) The few other quantitative data sets of liana density, though rarely directly comparable, tend to support our generalization. Putz (1982), using a very different technique to measure liana frequency, reports 231 lianas  $\geq$  2 cm diameter per ha on Barro Colorado Island, Panama, where he found that 43%–47% of the trees  $\geq$  20 cm diameter carried lianas. In the same forest

Montgomery and Sunquist (1978) found that approximately 50% of the trees  $\geq 15$  cm dbh carried lianas. At San Carlos de Rio Negro, Venezuela, in the poor soil region of central Amazonia, Putz (1982) found a similar value of 42% of trees  $\geq 10$  cm dbh carrying lianas. In contrast, Fox (1969) reported a value very similar to those of our Bornean samples of only 39 lianas  $\geq 2.5$  cm diameter per 1,000 m<sup>2</sup> for a 4-ha sample in Sabah. The Sungei Tekam Forest Reserve in Pahang, peninsular Malaysia, though having more lianas than our Bornean sites or those reported by Fox (1969), has fewer large climbers than Panama (F. E. Putz, personal communication; F. E. Putz, S. Apanah, and B. Mohamad, in prep.). Similarly, relative biomass of lianas, though declining on white sand soils on all continents, tends to be lower on oxisols in Southeast Asia than in the Neotropics, ranging from 2% in a Malaysian high dipterocarp forest to 5% in a Thai seasonal evergreen forest as compared to values of 4% to 7% for terra firma forests in Amazonian Venezuela and Brazil (Putz 1982, table 2.2). In sum, the available evidence strongly suggests intercontinental differences in forest structure over and above the site-specific variation.

Are these intercontinental differences in forest structure and vertebrate locomotory adaptation spurious correlations? One prediction from our hypothesis is that the distribution of gliding membranes and prehensile tails in marsupials of the Australian family Phalangeridae will be similarly correlated with vegetation structure. This family includes eight genera (29 spp.) with prehensile tails, three prehensile-tailed gliding genera (4 spp.), and one exclusively gliding genus (3 spp.). The large gliders are tropical forest folivores like all large gliders, but the smaller animals have a wide range of food habits. Eleven phalanger genera inhabit sclerophyllous Australian eucalyptus forest or scrubland; five of these (including only 1 glider) also have species on more densely forested New Guinea, and only one monotypic genus is restricted to New Guinea. As would be expected from the correlation of gliding and open forests, most gliding phalangers are found in Australian sclerophyll forest, which is open and virtually lacking in lianas (AHG, personal observation), rather than in relatively closed-canopy rainforest.

#### SUMMARY

Prehensile tails and gliding have arisen only in certain taxonomic groups which could occur only on certain continents as a result of biogeographic history, e.g., no marsupials in Africa or flying squirrels in the Neotropics. However, the simultaneous occurrence of these adaptations in a number of unrelated vertebrate families in some regions but not in others, even when the same families are present, and the parallel appearance of the same characters in ecological equivalents belonging to different orders or families (e.g., *Manis* and *Tamandua*; *Potos* and *Arctictis*; and *Anomalurus*, *Petaurista*, *Schoinobates*, and *Cynocephalus*) suggests that the biogeographic patterns of these adaptations are the result of more than chance.

Empirical evidence suggests that different forest structures in different parts of the world are correlated with different modes of locomotion by arboreal vertebrates. We suggest that scarcity of lianas in tropical Asia favors the long-distance

strategy of gliding; high liana frequency in tropical Africa correlates with a lack of specialized locomotory adaptations for inter-tree movement; many palms, an intermediate number of lianas, and perhaps generally more fragile branches in the Neotropics are associated with prevalence of prehensile tails.

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