6 EVOLUTIONARY TRENDS IN THE ECOLOGY OF NEW WORLD MONKEYS INFERRED FROM A COMBINED PHYLOGENETIC ANALYSIS OF NUCLEAR, MITOCHONDRIAL, AND MORPHOLOGICAL DATA

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The New World monkeys (Order Primates, Infraorder Platyrrhini) arose soon after African primates invaded South America some 25 million years ago (Figure 6.1; see Hoffstetter 1972, 1980; Martin 1990; Kay et al. 1997). They subsequently underwent extensive taxonomic diversification coupled with a spectacular adaptive radiation in diet, body size, feeding strategy, and mode of locomotion (Table 6.1). They now include roughly 80 of the 250 primate species worldwide (Mittermeier 1996). New World monkeys range throughout tropical America from Southern Mexico to northern Argentina, inhabiting steamy lowland rain forests, cool cloud forests, seasonally arid dry forests, and sun-baked savannas. They feed on fruits, leaves, nectar, plant exudates, insects, and vertebrates; some are specialized to exploit one or a few of these resources, while others are more generalized (Table 6.1). Most species are active diurnally, except the owl monkey, which is nocturnal over most of its geographical range. Within genera, most species and subspecies are allopatric and show relatively little ecological and morphological divergence from each other, in contrast to the striking divergence seen between genera in these respects. Body size ranges from 120 g to 12 kg; genera characterized by smaller body sizes tend to have more species and subspecies than larger-bodied forms.

Inferences about the adaptive radiation of New World monkeys from ecological and morphological points of view have been derived, so far, solely from phylogenies based on morphological data. Recently, however, extensive data on DNA sequences have become available (e.g., see Schneider et al. 1993, 1995; Harada et al. 1995; Horovitz and Meyer 1995; Meireles et al. 1995) that – when added to existing morphological data – change the inferred phylogeny of New World monkeys and provide a basis for new inferences about their pattern of morphological and ecological evolution. In recent years, several authors have published phylogenetic studies on subsets of New World monkeys, including Goeldi's monkey, marmosets and tamarins (callitrichins, including 5 genera and 32 spp.), howler, spider, woolly, and woolly spider monkeys (atelines, including 4 genera and 14 spp.), sakis and uakaris (pithecins, 3 genera and 9 spp.), owl and titi monkeys (2 genera, 19 spp.), and capuchin and squirrel monkeys (2 genera, 7 spp.), as well as some studies that encompass the whole radiation (e.g., see Rosenberger 1992; Ford and Davis 1992). This paper presents an evolutionary synthesis based on an analysis of combined DNA sequence and
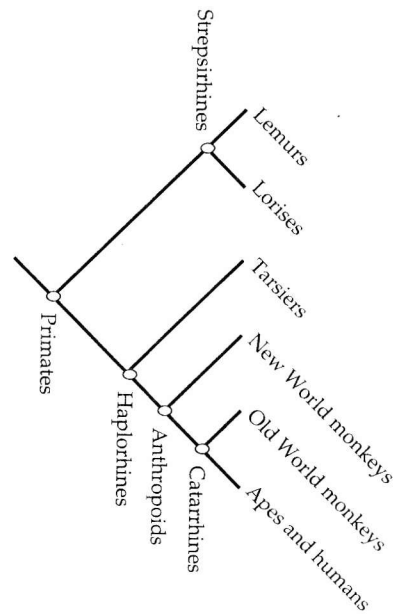
Figure 6.1. Phylogenetic tree of the order Primates, based on several lines of evidence and showing the common names associated with widely recognized clades mentioned in the text.

morphological data, and tests hypotheses about the adaptive radiation of the entire group and each nested subgroup of New World monkeys.

An important question in this kind of study is what data should be included in the phylogenetic analysis. For a character to evolve, it necessarily has to be heritable and therefore have the possibility of containing phylogenetic information. This, in turn, is a good reason to include every heritable character in a phylogenetic analysis. It has been argued that a character's evolution should be analyzed only on phylogenies that are independent of that character, and therefore that the character to be analyzed should be excluded from the phylogenetic analysis (see Avise 1994; Meyer et al. 1994). Here we argue that if the phylogeny changes its topology when the character in question is excluded, more data are necessary before the evolution of this character can be studied, until the topology is stable including or excluding the character in question. A character is evidence; if we exclude evidence from a phylogenetic analysis and obtain a different answer, then the answer with less evidence is likely not to be as reliable as the one based on more evidence.

After providing an overview of phylogenetic methods, we introduce the study organisms and summarize relevant ecological data collected from the literature, including habitat, diet, and locomotory and positional behavior (not all data are available for all genera, however), and then turn to an analysis of their adaptive radiation. The importance of different morphological characters and locomotory or positional behaviors in enabling different monkeys to exploit environments different from those exploited by platyrrhines (or their closest relatives) is an important point in our analysis. We will, also, discuss the plausibility and parsimony of character functions in the ancestors given the current roles of those structures.

Diet, locomotory and positional behavior, diurnality and nocturnality are all aspects in which New World monkeys have diversified extensively in comparison with catarrhines and suggest that they underwent an adaptive radiation following

Table 6.1. Species diversity, body size, diet, ecological distribution, and range of the genera of New World monkeys.[1]

Subfamily/tribe	Genus	Common name	Numbers of spp. (subspp.)	Body mass (g)	Diet	Habitats	Geographical distribution
Atelinae	Ateles	Spider monkey	4(16)	7,456 – 9,000	Fruits and leaves	Tall, mature forest with continuous canopy	Southern Mexico to central Bolivia and Brazil
	Brachyteles	Woolly spider monkey	1(1)	9,450 –12,125	Fruits and leaves	Coastal forest	Restricted area of Atlantic coastal forest of southeastern Brazil
	Lagothrix	Woolly monkey	2(5)	5,750 – 10,000	Fruits and leaves; in exceptional populations, insects	Tall, mature forest with continuous canopy	Central Colombia and a small portion of Venezuela, throughout the upper Amazonian basin, as far south as northern Bolivia
	Alouatta	Howler monkey	7(14)	4,550 – 11,352	Leaves and fruits	Wide spectrum of environments, including savannas	Southern Mexico to northern Argentina
Pithecinae	Callicebus	Titi monkey	10(16)	800 – 1,325	Fruits and either insects or leaves as secondary food	Primary forest, varillal and palm forest	Central Colombia and Venezuela to Paraguay
	Pithecia	Saki	5(8)	1,515 – 2,795	Fruits	High primary forest of terra firme	Western Amazonian region and Guianas
	Cacajao	Uakari	2(6)	2,740 – 3,450	Fruits	Floodplains	Western portion of Amazonian basin
	Chiropotes	Bearded saki	2(4)	2,510 – 3,100	Fruits	High primary forest of terra firme	Eastern portion of Amazonian basin
Aotinae	Aotus	Owl monkey	9(11)	690 – 1,232	Fruits; insects and leaves as a complement	Most forested areas and marginal areas	Panama to northern Argentina, absent in Guyana Shield and Atlantic and Paranense forests
Cebini	Cebus	Capuchin monkey	5(21)	2,220 – 3,868	Fruits and animals	Primary and secondary forest	Belize to northern Argentina
	Saimiri	Squirrel monkey	2(12)	695 – 932	Fruits and animals	Primary and secondary forest	Southern Costa Rica and Panama, central Colombia to Bolivia and northeastern Brazil
Callitrichini	Callimico	Goeldi's monkey	1(1)	483 – 502	Diet virtually unstudied, includes insects	Shrub and bamboo forest	Patchy distribution in the upper Amazonian basin; southern Colombia to northern Bolivia
	Callithrix	Marmoset	15(19)	182 – 429	Fruits, insects and exudates	Terra firme, disturbed areas, secondary forest	Eastern Bolivia and Brazil south of the Amazon and east of the Rio Madiera
	Cebuella	Pygmy marmoset	1(1)	126 – 130	Insects and exudates. Fruits are a minor component of their diet	Edges and interiors of seasonally inundated mature floodplain forests and mature nonflooded forests	Upper Amazonian basin, southern Colombia to northwestern Bolivia
	Leontopithecus	Lion tamarin	3(4)	535 – 615	Fruits, insects and plant exudates	Coastal lowlands, inland or low inundated forests	Four restricted areas in southeastern Brazil in the Atlantic coastal region and the Rio Parana basin
	Saguinus	Tamarin	12(33)	403 – 740	Insects, fruits, nectar and plant exudates	Terra firme, disturbed areas, secondary forest; some species in primary forest	Amazonian basin, Panama, and northwestern Colombia

[1] Sources: systematics from Mittermeier et al. (1988); body mass from Fleagle (1988; in prep.) and Ford and Davis (1992); geographic distribution from Wolfheim (1983) and Rylands et al. (1993); sources for habitats and diets in text.

their colonization of the New World (Fleagle 1988). We will use the concept of a "key innovation" or "evolutionary novelty" (Mayr 1963) when there is evidence that the function of the character in question is related with the use of a new range of resources or substrates.

Phylogenetic analysis

Analyses were conducted at the generic level, including all 16 genera of living New World monkeys plus one fossil taxon (*Cebupithecia sarmientoi*) from the late Miocene of La Venta, Colombia (Stirton 1951; Stirton and Savage 1951). Genera of New World monkeys are well-defined clades, whereas the limits between species and/or subspecies are frequently debated (see Napier 1976; Groves and Ramírez-Pulido 1982; Hershkovitz 1983, 1984; Ayres 1985; Thorington 1985; Ford 1994). There are at least 16 fossil genera of New World monkeys, most of which are very poorly known. The phylogenetic position of most of these is currently under debate, and when included in a cladistic analysis the large number of missing characters increases dramatically the number of most parsimonious trees (Novacek 1992, 1994; Forey, pers. comm.). We chose to include only one fossil taxon in our analysis, because its morphology is fairly well known and its phylogenetic position relatively stable.

Outgroups used included representatives of each of the major lines of haplorhinine primates: tarsiers (*Tarsius*), macaques (*Macaca*)/proboscis monkeys (*Nasalis*), gibbons (*Hylobates*), humans (*Homo sapiens*), and the fossil anthropoids *Aegyptopithecus*, *Apidium*, and *Parapithecus* from the Oligocene deposits of Fayum, Egypt (Simons 1962, 1965, 1987; Kay et al. 1981; Fleagle and Kay 1987). Molecular and morphological characters about which we had no information were scored as missing data.

Data used to estimate phylogeny included (i) nuclear DNA sequences of the ε-globin genes (Schneider et al. 1993) (261 informative characters) and interphotoreceptor retinol-binding protein (IRBP) gene, intron 1 (Harada et al. 1995) (332 informative characters); (ii) a fragment of the mitochondrial DNA sequence for the 16S ribosomal gene (Horovitz and Meyer 1995) (142 informative characters); and (iii) 66 morphological characters (see Appendix 6.1).

DNA sequences were aligned using Malign 1.89 (Wheeler and Gladstein 1993). Phylogenetic analyses were conducted using the heuristic algorithm in PAUP 3.1.1 (Swofford 1993), with 50 replicate searches based on randomly assembled starting trees. Bootstrap values for the cladogram obtained from combining all three data sets (the "total evidence" tree [Kluge 1989; Kluge and Wolf 1993]) were also obtained using PAUP, with 1,000 replications. Aligned sequences are available from the authors upon request. Entire gaps were considered characters, not each position separately, and gaps with different lengths were coded in sections. For example, given the alignment in Table 6.2, we distinguish three different gaps at (a) positions 5–7; (b) positions 8–11; and (c) positions 12–15. We cannot know how many events actually happened to create these gaps; there is a large number of possibilities. For example, each position could have undergone a single deletion event, gaps (a) and (b) could have been a single deletion event in taxa B and C, and so forth. According to the auxiliary

Table 6.2. Hypothetical DNA sequences used to illustrate the scoring of gaps in this study (see text).

Taxon	Position	Gap(s)
	1111111111122222222	
	1234567890123456789012345678901234567	
A	CTTAAACCGTGTGTACTGGGAGAACCA	
B	CTTA—— —— —— CTGGGAGAACCA	abc
C	CTTA—— —— —— CTGGGAGAACCA	abc
D	CTTAAAC—— —— CTGGGAGAACCA	bc
E	CTTAAAC—— —— CTGGGAGAACCA	bc
F	CTTAAAC—— —— CTGGGAGAACCA	bc
G	CTTAAACCGTG—— CTGGGAGAACCA	c
H	CTTAAACCGTG—— CTGGGAGAACCA	c
I	CTTAAACCGTGTGTACTGGGAGAACCA	

principle of Hennig (1966), we will consider gaps in the same positions across taxa as homologous, and therefore we consider gap (a) homologous in B and C, gap (b) homologous in B through F, and gap (c) homologous in B through H. Distinguishing gaps (a), (b), and (c) allows us to capture all the information contained in these alignments and to postulate the smallest number of insertion-deletion events possible, which is the most parsimonious hypothesis.

Nuclear, mitochondrial, and morphological data sets were analyzed separately first, and yielded different topologies (Figure 6.2). The consistency index (CI) and tree length (L) excluding uninformative characters for each tree were as follows: CI = 0.63, L = 1,208 for nuclear DNA; CI = 0.47, L = 506 for mitochondrial DNA; and CI = 0.56, L = 214 for morphological data. The nuclear and morphological trees showed the most congruent topologies. Analysis of the combined data yielded a single tree with CI = 0.57 and L = 1,953 (Figure 6.3). The topology of this tree is not perfectly congruent with that resulting from any of the individual data sets, but most branches of the total evidence tree are supported by each data set. There are three notable exceptions: nodes 1, 2, and 3 are not supported by morphology. When morphological characters are excluded, the topology of the total evidence tree does not change.

Support for the position of the owl monkey (*Aotus*) relative to the capuchin and squirrel monkeys (*Cebus, Saimiri*) and the callitrichins is weak; the completely resolved topology presented (Figure 6.3) is only two steps shorter than the grouping of the owl monkey with either callitrichins or with the capuchin-squirrel monkey dyad; the bootstrap tree does not resolve these relationships. The degree of incongruence between data sets (Mickevich and Farris 1981; Kluge 1989) was very low. The total number of extra steps in the total evidence tree was 833, accounted for by incongruence within and between data sets. Only 25 of them were generated by incongruence between data sets, which represents 3% of the total incongruence. All three data sets required extra numbers of steps when overlaid on the total evidence tree,
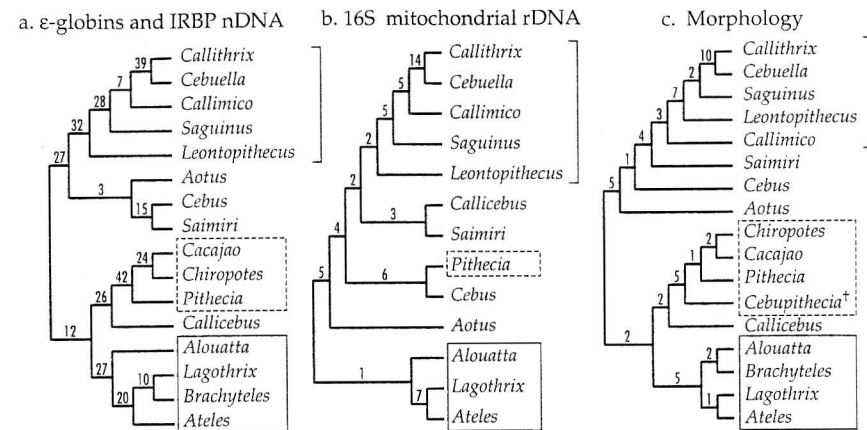
Figure 6.2. Cladograms obtained with (A) nuclear sequences of ε-globins (Schneider et al. 1993) and IRBP (Harada et al. 1995) and realigned with Malign, CI = 0.63; (B) 16S mitochondrial rDNA sequences (Horovitz and Meyer 1995), CI = 0.47; and (C) morphological characters, CI = 0.56 (see Appendix). All consistency indices shown exclude uninformative characters. The number of unambiguous character-state changes is indicated above each branch. Callitrichins are demarcated with a bracket, and pithecins and atelines are enclosed in a dashed and a solid rectangle respectively. †Indicates fossil taxa.
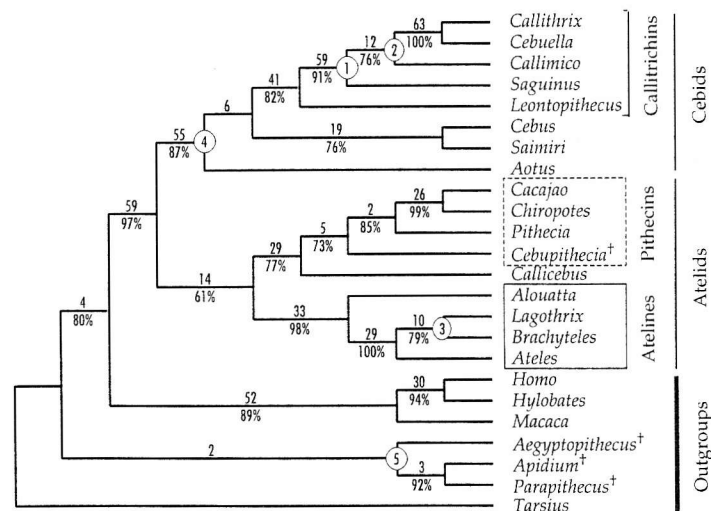

Figure 6.3. Total evidence cladogram (CI = 0.57) obtained by analyzing the combined data from ε-globins (Schneider et al. 1993), IRBP (Harada et al. 1995), 16S mitochondrial rDNA (Horovitz and Meyer 1995), and morphology (see Appendix). Nodes 1, 2, and 3 have no support from morphological characters. Numbers below the branches indicate level of bootstrap support; numbers above branches indicate branch lengths. The bootstrap tree does not support nodes 4 and 5. The two basal platyrrhine clades are Atelidae and Cebidae. The consistency indices, excluding uninformative characters, for the various data sets overlaid on the total evidence tree are 0.63 for nuclear DNA sequences, 0.46 for mitochondrial DNA sequences, and 0.53 for morphology. †Indicates fossil taxa.

relative to the most parsimonious tree based on each data set separately: the nuclear data set required 1 extra step (relative to 593 informative characters), the mitochondrial 11 extra steps (relative to 142 informative characters), and the morphological 11 extra steps (relative to 66 informative characters).

Different data sets reflect a shared history, so the phylogenetic signal they contain should be the same, even if it is obscured by homoplasy. On the other hand, the distribution of homoplasy is likely to be different for each data set, given that each is subject to different constraints (e.g., those pertaining to function). If the data sets are combined, the signal common to all of them is more likely to overwhelm the homoplasy than if each is analyzed separately. Whether this approach is always appropriate is still being debated (Kluge 1989; Kluge and Wolf 1993; Donoghue and Sanderson 1992; Bull et al. 1993; Chippindale and Wiens 1994; Huelsenbeck et al. 1994; Funk et al. 1995; Lockhart et al. 1995; see Chapters 1 and 2 in this volume).

Adaptive radiation in the New World monkeys

The implications of our phylogeny for the interpretation of the adaptive radiation in the New World monkeys are summarized below. The taxonomic categories used are based on Rosenberger (1979) but adjusted to the topology of our preferred tree: the family Atelidae includes subfamilies Atelinae and Pithecinae; its sister-group, the family Cebidae, includes subfamilies Aotinae and Cebinae. The last group contains the tribes Callitrichini and Cebini. For each group, we discuss the implications of our phylogeny for systematic relationships and for shifts in diet, habitat, mode of locomotion, and positional behavior.

Atelidae (Atelinae, Pithecinae)

SYSTEMATICS – This clade is supported by two unambiguous morphological characters: reduction of the pterygoid fossa, and a deciduous lower second premolar with a rounded outline, derived from a mesiodistally elongated outline. The basal dichotomy of this clade implies that the Atelinae and Pithecinae are sister clades.

Atelinae (*Alouatta*, [*Ateles*, {*Lagothrix*, *Brachyteles*}])

SYSTEMATICS – The Atelinae includes the howler (*Alouatta*), spider (*Ateles*), woolly (*Lagothrix*), and woolly spider (*Brachyteles*) monkeys. Three morphological characteristics are unique to atelines among New World monkeys: a prehensile tail covered ventrally by bare skin with friction ridges; a large body; and very long forelimbs relative to hindlimbs (Erikson 1963). They show some convergences with extant apes in their limb and trunk morphology, which are probably related to suspensory habits (Erikson 1963). An ateline can support the weight of its suspended body by its tail.

Relationships within atelines in the nuclear DNA sequence data trees (ε-globin genes, Schneider et al. 1993; γ-globin genes, Meireles et al. 1995; IRBP gene, Schneider et al. 1995 and Harada et al. 1995) and the total evidence tree (Figure 6.4) differ from previous hypotheses: (*Alouatta*, [*Ateles*, {*Lagothrix*, *Brachyteles*}]). We designate the clade composed of the latter three taxa as the Atelini. Members of this group have only four
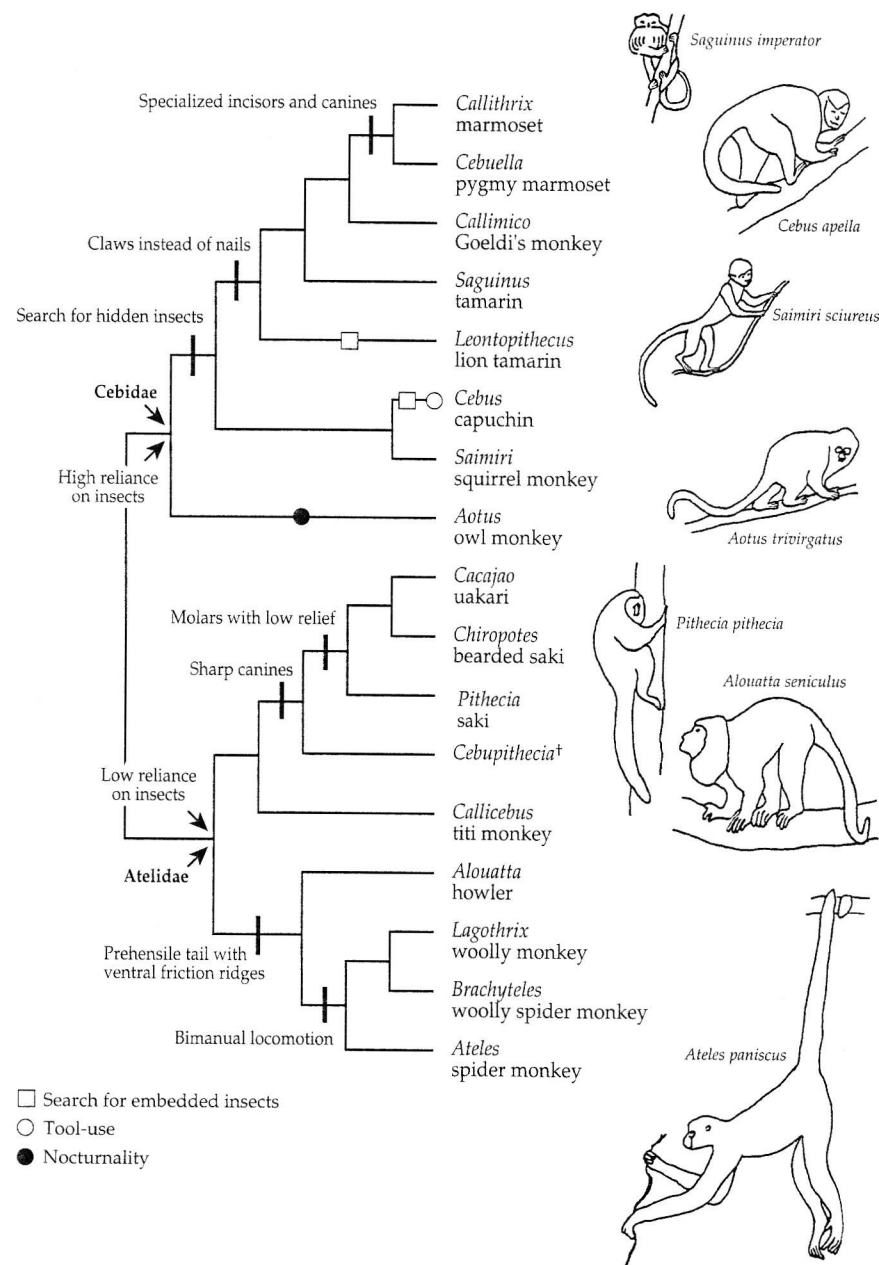
Figure 6.4. Overlay of key morphological innovations and inferred ecology of ancestral forms on the total-evidence phylogeny. Synapomorphies are indicated by vertical bars and associated labels; special symbols (see legend) mark the autapomorphies.

lumbar vertebrae and large ratios of hindlimb relative to trunk length. In contrast, howler monkeys have a mode of five lumbar vertebrae and a smaller hindlimb ratio, falling roughly between that of the owl and the capuchin monkey (Erikson 1963), plus a number of other postcranial synapomorphies listed by Ford (1986b).

Erikson (1963) found several derived characters shared by spider monkeys and woolly spider monkeys, including a reduced thumb (nearly or completely absent as an external character) and a very short lumbar region relative to thoracic length (in terms of both the number and size of individual vertebrae). A few dental characters are shared by the howler monkeys and woolly spider monkeys, such as the presence of a mesoloph on the first upper molar (Zingeser 1973; MacPhee et al. 1995). A mesoloph is a large crest, usually presented as an adaptation for masticating leaves. Under the total evidence tree topology, these characters are either homoplasies, as in the case of characters shared by the howler and woolly spider monkeys, or of ambiguous optimization, as in the case of those shared by the spider and woolly spider monkeys. In other words, the latter are either convergences between the spider and woolly spider monkeys, or have been acquired by the common ancestor of spider, woolly, and woolly spider monkeys and secondarily lost by the woolly monkey.

HABITAT, LOCOMOTION, AND POSITIONAL BEHAVIOR – Howling monkeys show the broadest geographic distribution, from southern Mexico to northern Argentina, and throughout the Amazon basin. They are everywhere sympatric with at least one other genus of atelines, except in the most extreme parts of their range. The woolly spider monkey has the most limited distribution; it occurs in a restricted area of the Atlantic coastal forest of southeastern Brazil. The spider and woolly monkeys occur primarily in tall mature forest with continuous canopy, while howler monkeys are found in a wide range of environments, including savannas (Fooden 1963; Fleagle and Mittermeier 1980; Peres 1990, 1994; Soini 1990; Stevenson et al. 1994). All atelines occur in the middle and high levels of the canopy (Mendel 1976; Fleagle and Mittermeier 1980; Gebo 1992; Defler 1995).

The spider, woolly, and woolly spider monkeys have the ability to travel with bimanual locomotion (brachiating and arm-swinging) and use relatively small supports. In contrast, howlers do not brachiate and travel mostly quadrupedally along bigger supports. Spider and howler monkeys climb frequently; when feeding, all genera use suspensory positions aided by their prehensile tail (Mendel 1976; Fleagle and Mittermeier 1980; Cant 1986; Gebo 1992).

DIET – Atelines are highly folivorous and frugivorous. Howlers are the most folivorous (Milton 1980) regardless of whether they are sympatric with other atelines; the woolly spider monkey is intermediate; and spider and woolly monkeys are mostly frugivorous (Strier 1992). Reports from different study sites are consistent for most species, except in the case of the woolly monkey, for which contrasting degrees of insectivory have been reported from different sites. *Lagothrix lagothricha lugens* was studied in La Macarena, Colombia and reported to eat mostly fruits (60% of its diet throughout the year) (Stevenson et al. 1994). Insects were the second most commonly consumed resource throughout the year (23%) at this single location. This degree of insectivory is unusually high for atelines, and contrasts sharply with reports on a population of *L. l. lagothricha* in Vaupes, Colombia. According to Defler (1995), the

diet of this population included 94.6% leaves and fruits (with no report on the remainder). Muñoz Durán (1991) stated this same population included insects in its diet, but provided no percentages. In the headwaters of the Urucu river in Brazil, *L. l. cana* fed on insects during only 0.1% of its feeding time (Peres 1994).

Pithecinae (*Callicebus, Pithecini*)

SYSTEMATICS – This clade is supported by the following unambiguous morphological synapomorphies: trigonid and talonid of subequal height in the lower second molar, and presence of prehypocrista on the first upper molar derived from a primitive condition of absence (subsequently reversed in living pithecins). Pithecines include the titi monkey *(Callicebus)* and the pithecins. The latter include four genera: *Cebupithecia* (fossil pithecin), sakis *(Pithecia)*, uakaris *(Cacajao)*, and bearded sakis *(Chiropotes)*. The sister-group relationship between the titi monkey and pithecins is supported by the total evidence, morphological and nuclear DNA trees. Rosenberger (1979, 1981, 1984) and Horovitz (1995, in prep.) presented hypotheses based on morphology that are closest to our total evidence tree; however the owl monkey *(Aotus)* does not appear to be sister to the titi monkey as Rosenberger (1984) suggested, but instead appears to be sister to the callitrichins, *Cebus*, and *Saimiri* (Figure 6.4).

Callicebus

HABITAT AND POSITIONAL BEHAVIOR – Titi monkeys are found from central Colombia and Venezuela to Paraguay. The yellow-handed titi *(C. torquatus)* forages in different varieties of varillal and palm forest (Kinzey et al. 1977; Kinzey 1977a). Varillal is a non-flooded forest with a relatively closed canopy, abundant vertical tree trunks (a characteristic from which its name is derived), and reduced undergrowth; it comprised 60% of the territory of the troop studied. While the yellow-handed titi forages mostly in the second and emergent stories of the forest canopy, *C. cupreus discolor* (sensu Mittermeier et al. 1988) is generally found lower in the forest (Kinzey 1978).

The most common feeding posture of the yellow-handed titi is sitting except if feeding on berries, when it adopts an erect posture, with the torso parallel to the vertical trunk and the feet inverted and powerfully adducted, with the pollex grasping the trunk (Kinzey 1977a,b).

DIET – Titi monkeys are primarily frugivorous but different species complement their diet in different ways. The second leading food item for yellow-handed titis (*C. torquatus*) are insects (14%) (Kinzey et al. 1977; Kinzey 1977a; Kinzey 1978), whereas that for *C. brunneus* and *C. personatus* are leaves (Kinzey 1978; Kinzey and Becker 1983; Wright 1989). *C. brunneus* spent 10 to 15% of its time sitting and scanning for insects and, although data on actual insect feeding bouts are unavailable, the success rate was apparently low (Wright 1989). The masked titi (*C. personatus*) has not been observed to eat insects (Kinzey and Becker 1983).

The yellow-handed titi opens hard husked fruits by placing them in the corner of its mouth, and cracking them with the canines or the premolars (Kinzey 1977a). Titis catch insects in the air, leaves, or at ant nests; only on rare occasions have they been observed to go down to the ground to obtain insects.

Pithecini (*Cebupithecia*, [*Pithecia*, {*Cacajao, Chiropotes*}])

SYSTEMATICS – Pithecini includes sakis *(Pithecia)*, uakaris *(Cacajao)*, bearded sakis *(Chiropotes)*, and the fossil *Cebupithecia*. The monophyly of this group is supported by the presence of a diastema between the lower canine and second incisor, a sharp lingual vertical edge on the lower canines, a reduction of the lower third molar relative to the length of the fourth premolar, proclivious upper incisors, and a high preparacrista on the upper third premolar. Monophyly of living pithecins is further supported by crenulated molar enamel and loss of a lingual cingulum on the fourth upper premolar. A sister-group relationship between uakaris and bearded sakis is supported by a buccolingual enlargement of the fourth upper premolar relative to the first molar, and the loss of the prehypocrista on the first upper molar.

HABITAT, LOCOMOTION, AND POSITIONAL BEHAVIOR – Pithecines live in the Amazon basin and the southern margin of the Orinoco river. Uakaris are always associated with floodplains, whereas bearded sakis live in areas of high primary forests of terra firme (relatively high non-flooded ground) (Fontaine 1981; Ayres 1989). Sakis seem to be the most flexible of the pithecins: they are found primarily in unflooded forest and they are sympatric over a large part of their range with bearded sakis; they overlap with uakaris in narrow bands of flooded forest (Peres 1993).

The white-faced saki (*Pithecia pithecia*) is predominantly a leaper, while bearded sakis and uakaris are primarily quadrupedal. Data on posture while feeding is more limited, but sakis frequently cling to trunks of trees or lianas, and uakaris and bearded sakis apparently feed more commonly in pronograde quadrupedal postures, and less commonly adopt hindlimb suspensory postures (Ayres 1986; Fleagle and Meldrum 1988).

Bearded sakis are upper- and middle-canopy frugivores (Norconk and Kinzey 1994); sakis have more varied habits. Where the white-faced saki (*P. pithecia*) co-occurs with bearded sakis (e.g., in the Guianas), it frequently feeds in the understory and the lower part of the canopy (van Roosmalen et al. 1988; Kinzey and Norconk 1993). On the other hand, where the white saki (*P. albicans*) occurs in the absence of other pithecines (e.g., in Amazonia), it is found mostly in the higher levels of the canopy (Peres 1993). Uakaris live in floodplains and surrounding terra firme, and descend to the ground when water levels drop in order to eat seeds and seedlings (Ayres 1989).

DIET – Pithecins are frugivores (at least 85% of feeding time), but differ from other frugivorous New World monkeys in exploiting unripe fruits, with a harder pericarp and a pulp with lower sugar content and more defensive compounds than ripe fruits. Biochemical analysis of the fruits eaten by sakis indicate that the preferred species have a high lipid content (47 to 50%) and therefore a high nutrient value (Kinzey and Norconk 1993). Pithecins also consume leaves and arthropods (Ayres 1986, 1989; Kinzey 1992).

Pithecins are seed predators, digesting the seeds they ingest. Their strategy contrasts with that of seed dispersers (e.g., spider monkeys) who feed on and digest the pericarp, in most cases the mesocarp, and/or the aril, and either drop the seed before ingestion or allow the seed to pass through their tract undigested. Seeds of consumed fruit are frequently protected by a hard covering (pericarp, usually a hard mesocarp, and/or sometimes the seed coat). Pithecins can break the hard husk with their specialized canines, discard the pericarp, and then masticate the seeds, which are actually

the protein-rich part of the fruits. Bearded sakis feed on the immature seeds of a large number of species that are consumed when mature by sympatric spider monkeys. The black-bearded saki (*Chiropotes satanas*) can open fruit with pericarp as much as 15 times harder than those opened by the black spider monkey (*Ateles paniscus*); and the average crushing pressure (2.77 kg mm^{-2}) exerted by the black-bearded saki is significantly greater than that (0.03 kg mm^{-2}) exerted by the black spider monkey (Kinzey and Norconk 1990). The average crushing resistance of seeds consumed by the black-bearded saki (7.2 ± 0.7 kg) is significantly smaller than that of seeds swallowed by the black spider monkey (17.1 ± 2.6 kg) (Kinzey and Norconk 1990). The hardness of fruits that sakis open is intermediate between those opened by spider monkeys and bearded sakis (Kinzey and Norconk 1990, 1993).

Cebidae (*Aotus*, [{*Cebus, Saimiri*}, Callitrichini])

SYSTEMATICS – This clade is composed of owl monkeys (*Aotus*), capuchin monkeys (*Cebus*), squirrel monkeys (*Saimiri*), and the callitrichins, which include Goeldi's monkey (*Callimico*), marmosets (*Callithrix* and *Cebulla*), and tamarins (*Saguinus* and *Leontopithecus*). The monophyly of callitochins has rarely been questioned, but its relationships to other New World primates has been widely debated. Rosenberger (1979, 1981, 1984) suggested that capuchins (*Cebus*) and squirrel monkeys (*Saimiri*) were sister-groups based on morphology; the same conclusion was reached by Schneider et al. (1993) based on nuclear DNA sequences, and by us (Figure 6.4) based on an analysis of combined molecular and morphological data. The only previous studies that have placed owl monkeys (*Aotus*) in Cebidae (as defined here) are Schneider et al. (1993), Harada et al. 1995, and Horovitz (1995), based on nuclear DNA sequences and morphological data. Our total evidence analysis (Figure 6.4) indicates that *Aotus* is sister to the cebids and callitrichins.

Aotinae (*Aotus*)

HABITAT – Owl monkeys are widespread from Panama to northern Argentina, and live in most forested areas except in the Guyana shield and the Atlantic and Paranense forests. They are also successful in certain seasonally arid environments, such as the Chaco in southern Paraguay and north-central Argentina. Owl monkeys are the only nocturnal members of Anthropoidea, including both Platyrrhini and Catarrhini (see Figure 6.1).

DIET – *Aotus nigriceps* in Cosha-Cashu National Park, Peru, eats mostly small ripe fruits, which it complements with insects and leaves; flowers and nectar are also consumed (Wright 1989). Owl monkeys forage for insects at dawn and dusk and during moonlit nights. They grab insects out of the air with one hand while walking along the branches of tall trees. Owl monkeys ingest more insects on a daily basis than sympatric titi monkeys, based on data from fecal samples (Wright 1989).

Owl monkeys are successful in certain habitats that are marginal for other primates, such as the Chaco. There it is sympatric with the black howler (*Alouatta caraya*) and, at least in some areas, the brown capuchin (*C. apella*) (M. Di Bitetti pers. comm.). Some aerial predators present in Amazonian Peru (e.g., harpy eagles and crested

eagles) are rare in the semi-arid Chaco, where the great horned owl is common (Wright 1989). Owl monkeys are not strictly nocturnal in Paraguay (Wright 1989) or Argentina (Arditi pers. comm.). They can commonly be seen foraging for 1 to 3 hours during the day; traveling and feeding can occur at any time of the day or night. In Paraguay, leaf-eating is higher (46%) than in Peru in winter, when fruits are scarce. During the spring, insect and flower consumption is very high (Wright 1989).

Cebini (*Cebus, Saimiri*)

SYSTEMATICS – Capuchin monkeys (*Cebus*) and squirrel monkeys (*Saimiri*) are sister taxa. This is supported by at least two morphological characters: the fourth upper premolar is wider than the first molar and the vomer is exposed in the orbit. Capuchin monkeys have a prehensile tail which can support the entire body weight for short periods of time in adults (10 to 15 s) and for longer periods (> 30 s) in juveniles (M. Di Bitetti and C. Janson, pers. comm.).

HABITAT, LOCOMOTION, AND POSITIONAL BEHAVIOR – *Cebus* is one of the most widely distributed genera of New World monkeys, ranging from Belize to northern Argentina. *Saimiri* occurs in Costa Rica and Panama, and ranges from central Colombia to Bolivia and northeastern Brazil. *Cebus* provide two of the few cases of congeneric sympatry: the tufted capuchin (*C. apella*) co-occurs over part of its range with the white-fronted capuchin (*C. albifrons*) or the wedge-capped capuchin (*C. nigrivitattus*). Capuchin and squirrel monkeys are both found in primary and secondary rain forests (Terborgh 1983; Boinski 1987, 1989b).

Capuchins show great variability in feeding heights in the forest (Terborgh 1983). Data on locomotor behavior of the white-throated capuchin (*C. capucinus*) indicate that it is highly quadrupedal (54%), and secondarily climbs (26%) and leaps (15%). Its positional behavior includes sitting (44%), standing (31%), and reclining (13%) (Gebo 1992). C. Janson (pers. comm.) has occasionally observed the tufted capuchin (*C. apella*) suspended from its tail when feeding on spiny palms.

Saimiri oerstedii typically forages and travels at about 5 to 10 m above the ground, on thin branches (< 5 cm diameter). Squirrel monkeys are basically quadrupedal, with a lower incidence of climbing or leaping and clinging on vertical thin substrates (Boinski 1987, 1989b). Its most common feeding postures are sitting, hanging by the hindlimbs, and sitting in tripod stance (i.e., on its hindlimbs while maintaining its tail as a third point of support on the substrate) (Boinski 1989b).

DIET – Capuchins and squirrel monkeys are mainly frugivorous but also rely heavily on other animals as source of protein (Janson and Boinski 1992). Capuchins also rely on other resources toward the margins of their distribution. For example, in some areas in northern Argentina, their primary resource is bromeliads; in other areas, they feed heavily on fruits during one season, but switch to insects at other times (Brown and Zunino 1992).

Capuchins can open hard husked fruits by holding them in their hands and biting them open, using incisors for smaller fruits (1–3 cm) and premolars or molars for larger fruits (Janson and Boinski 1992). Capuchins are a pre-dispersal seed predator of *Cariniana micrantha*, an emergent member of the Brazil-nut family Lecythidaceae (Peres 1991).

Callitrichini (*Leontopithecus*, [*Saguinus*, {*Callimico*, (*Callithrix*, *Cebuella*)}])

SYSTEMATICS – The Callitrichini is composed of five genera: Goeldi's monkey (*Callimico*), the marmosets (*Callithrix*, *Cebuella*), and the tamarins (*Leontopithecus*, *Saguinus*). Characteristics of this group are that they are among the smallest of the anthropoids, and in absolute terms have the smallest brain volumes; they bear claws on all manual and pedal digits except the hallux. Within this group, the only point on which both morphological and molecular analyses agree is the sister-group relationship between the two genera of marmosets. The most common hypothesis based on morphology alone is that Goeldi's monkey is the earliest diverging taxon of callitrichins (Rosenberger 1981, 1984; Ford 1986b; Kay 1990; this paper). On the other hand, analyses based on DNA and amino-acid sequences (Schneider et al. 1993; Horovitz and Meyer 1995), immunological data (Sarich and Cronin 1980), and cytogenetic data (Seuanez et al. 1989) suggest that Goeldi's monkey is closely related to the marmosets. Some studies suggest the tamarins are monophyletic, but others (including our total evidence analysis, see Figure 6.4) do not.

In addition to the unreversed characters mentioned above, Callitrichini is supported by (i) reduction of the size of the pterygoid fossa from reaching the base of the skull to a shallow space between the lateral pterygoid process and the splinterlike medial process; (ii) loss of the third molar; (iii) loss of hypocone on the first upper molar; and (iv) two offspring at a time (from a primitive condition of one). All four characters are reversed in Goeldi's monkey. No unambiguous morphological characters support nodes 1 and 2 (Figure 6.3). Morphology strongly indicates a basal position for Goeldi's monkey within callitrichins, but this signal is overwhelmed by molecular characters indicating its position as sister to the marmosets. Marmosets share several specializations such as staggered lower incisors of equal height which display meso- and distostyles, mesiodistally compressed canines, and buccolingually compressed deciduous lower incisors.

Lion tamarins have acquired certain specializations, unique among anthropoids, that have been associated with their outstanding manipulative abilities; they have long and slender arms and hands, and partially webbed middle fingers that they use to probe for and extract prey (Coimbra-Filho 1970b; Hershkovitz 1977).

HABITAT, LOCOMOTION, AND POSITIONAL BEHAVIOR – Callitrichins range from southeastern Costa Rica (tamarins) to Bolivia (Goeldi's monkey and marmosets) and southeastern Brazil (lion tamarins). Traits all callitrichins share are the exploitation of low levels of the canopy and understory, and the ability to cling onto big trunks and large branches for feeding and/or traveling purposes. The marmoset *Callithrix* and the tamarin *Saguinus* occur in "terra firme" and are generally absent from floodplains. They use disturbed, edge, or secondary growth forest, except some species of *Saguinus* that also live in primary forests (Rylands 1986; Garber 1993). The habitats of the pygmy marmoset (*Cebuella*) are the edges and interiors of seasonally inundated mature floodplain forests, although it also occurs in mature non-flooded forest (Moynihan 1976b; Soini 1993; Hernández-Camacho and Cooper 1976). Lion tamarins live in coastal lowlands, inland Atlantic forests, and low inundated forests (Coimbra-Filho 1970a,b; 1976). The forests occupied by all species except *L. chrysopy-*

gus chrysopygus have abundant epiphytic bromeliads, a common foraging substrate (Rylands 1993). Goeldi's monkey lives in scrub forest, mostly low and young second growth and in bamboo forests (Moynihan 1976a; Izawa 1979b; Pook and Pook 1981; Buchanan-Smith 1991), although it is also found in primary forest (Christen and Geissmann 1994).

Saguinus fuscicollis, *S. geoffroyi*, *S. mystax*, and *S. midas midas* travel mostly quadrupedally, climbing, and leaping (Fleagle and Mittermeier 1980; Garber 1991; Garber and Pruetz 1995). In *S. fuscicollis*, 20% of leaps involve moderate- to large-sized vertical trunks, which are rare in *S. geoffroyi* and *S. mystax* (Garber 1991). Lion tamarins seem to have a pattern of locomotion like that of *Saguinus* excluding *S. fuscicollis* (Coimbra-Filho and Mittermeier 1973). *Cebuella* and *Callimico* leap frequently to and from vertical trunks (Kinzey et al. 1975; Moynihan 1976a,b; Pook and Pook 1981). *Cebuella* spends 77% of its feeding time clinging onto trunks (Kinzey et al. 1975). *Callithrix* probably has very similar locomotor and positional habits, although no quantitative data are available for this genus.

DIET – Marmosets and tamarins feed on plant exudates (sap, gum, resin) as a complement to fruits and insects (Sussman and Kinzey 1984; Ferrari and Lopes Ferrari 1989; Soini 1993). Marmosets possess specialized incisors which they use for gouging holes in tree bark and directly stimulating the flow of gum, and spend a considerably higher percentage of their time feeding on this resource than tamarins. *Leontopithecus rosalia* has also been observed to chew on bark to stimulate gum flow (Peres 1989), despite the fact that it does not possess specialized incisors. *Saguinus* relies on natural damage to the bark or the activity of wood-boring insects to obtain gums.

Lion tamarins forage for insects in a manipulative fashion and catch mainly nonmobile prey concealed in palm crowns, bromeliad axils, wooden crevices, and under bark (Garber 1992; Rylands 1989). *Saguinus* forages for insects on the surface of branches and in vine tangles and foliage under the canopy and *Saguinus fuscicollis* in addition explores tree-trunk bark (Garber 1992). Information on the diet of Goeldi's monkey is limited, and there are no year-round field studies. It feeds on insects in a strategy similar to that of *S. fuscicollis* and *nigricollis* (Garber 1992).

Evolutionary patterns of ecological specialization

The first cladogenetic event in the platyrrhine ancestral lineage gave rise to two successful and diverse groups, the Atelidae and Cebidae (Figure 6.4). No obvious basal morphological innovations appeared in these two clades that allowed them to exploit new resources. Atelidae is comprised of atelines (howler, spider, woolly, and woolly spider monkeys), pithecins (sakis and uakaris), and the titi monkey; Cebidae is comprised of the owl, capuchin, and squirrel monkeys, as well as the callitrichins. The most noticeable ecological difference between the Atelidae and Cebidae is the highly herbivorous diet of virtually all species in the former, and a higher reliance on insects in the latter (Rosenberger 1981, 1992). In the Atelidae, pithecines and atelines generally feed at least 94% of the time on plants (Kinzey 1978, 1992; Rosenberger and Strier 1989). The known exceptions are one population of *Lagothrix lagothricha* and one of *Callicebus torquatus* that feed on insects a high proportion of the time (23 and 14%, respectively).

Cebidae is characterized by a higher consumption of insects than most Atelidae. The heavy consumption of insects by owl monkeys has been attributed to their activity at night when insects are most active (Kinzey 1992). However, insect consumption also seems to be high in areas where owl monkeys are more active during the daylight hours (Wright 1989). The primary food for squirrel monkeys is sometimes insects (Boinski 1989a; Janson and Boinski 1992). Capuchins rely less on insects than squirrel monkeys do; for example, the tufted capuchin (*C. apella*) spends about half of its day manipulating substrates and ingesting prey (Janson 1990) and obtains approximately 16% of its energy from insects (Janson 1985; Janson and Boinski 1992). Callitrichins also rely heavily on insects; according to most reports, they spend more than 13% of their time foraging for insects.

Besides diet, Atelidae and Cebidae generally differ in body weight. Body weight varies from 0.13 to 3.8 kg in Cebidae, and from 1.3 to 12 kg in Atelidae. Curiously, the species with the extreme body weights in either group belong to genera that are deeply nested in the phylogeny: there has been a certain tendency towards reduction in body size in Atelidae, and towards enlargement in body size in Cebidae.

Across primates generally and in New World monkeys in particular, the reliance on animal prey (or other food items of high energy content) decreases with increasing body size (see Ford and Davis 1992). However, within smaller groups the pattern is not always so clear. Within callitrichins, for example, there is no direct relationship between body size and degree of insectivory or exudativory (Garber 1992). The relationship between body weight and diet has traditionally been explained in terms of metabolic rates. Smaller species have higher metabolic rates than larger ones, and therefore the expectation is that they need to consume a higher proportion of energy-rich resources to support their higher needs (Kleiber 1947, 1961; Clutton-Brock and Harvey 1983; Eisenberg 1981, 1990; Martin 1990; Schmidt-Nielsen 1984; Kay 1984; Ford and Davis 1992).

In spite of the apparent absence of key morphological innovations for the Atelidae and Cebidae, subclades of these broad groups seem to have evolved traits that enable them to exploit resources that may not be accessible to other groups, based on the nature of those resources or their arboreal location. This functional radiation may have increased the number of species that can coexist locally, and is discussed below.

Atelinae

ATELINES – the howler, spider, woolly, and woolly spider monkeys – possess an apparent key innovation, a prehensile tail, that opens the possibility of exploiting a range of resources inaccessible to other quadrupeds. Tail prehensility has evolved independently in six orders of mammals with very different ecological roles (e.g., frugivory, folivory, and omnivory), in such groups as the opossums, kinkajous, porcupines, and primates. All use their prehensile tails both for support while feeding on branch-tips or locations of difficult access and as an aid in locomotion, especially on unstable supports or while descending (Grand 1978; Charles-Dominique et al. 1981; Emmons and Gentry 1983). Emmons and Gentry (1983) noted that prehensile-tailed animals occur with a higher frequency in neotropical forests than in Africa or Asia.

Moreover, use of the prehensile tail to move through the canopy seems mostly restricted to the Neotropics (Emmons and Gentry 1983). Tropical forests are thought to be structurally similar across continents (Richards 1952; Leigh 1975), based mostly on measures of biomass and productivity, leaf size and shape, canopy height and degree of stratification, and tree density (Dawkins 1959; Leigh 1975). However, Emmons and Gentry (1983) reasoned that there might be some differences that make the possession of a prehensile tail advantageous in the Neotropics and not the Paleotropics. With the purpose of investigating this question, they quantified several factors, and found two interesting differences: (1) liana density is higher in Africa than in the Neotropics and Borneo; and (2) there are more palm trees in South American forests than on the other continents.

Lianas have two important functions for monkeys, providing food and travel corridors. Prehensile tails are probably not of much use when traveling on lianas (Emmons and Gentry, 1983). But they may be particularly useful in coping with the downward bending of branch tips under the weight of suspended animals. When lianas are present, animals tend to use them to pass from one tree to another, which allows them to bypass droop-prone terminal branches. Therefore, it seems that the extensive presence of lianas in Africa may have reduced the usefulness of prehensile tails.

The second variable considered by Emmons and Gentry (1983) is the frequency of palms, which is far greater in neotropical forests. Palms are rarely invaded by lianas (Putz 1980) and are often surrounded by gaps in the vegetation. Arboreal animals frequently use palms as a pathway through the forest, and some eat palm fruits. Those animals who have prehensile tails use them to gain access to the palm trees. Emmons and Gentry (1983) postulated that frequent climbing on palm trees may have contributed to the selective advantage of prehensile tails in the Neotropics.

Atelines use suspensory feeding postures with the aid of their tail, spreading their weight over several widely dispersed supports, hanging by their long limbs and tail. This allows them access to resources on branches that would be too thin to support their large body weight if they were to stand on them. Spider monkeys (and probably woolly and woolly spider monkeys) travel along smaller supports than one would expect based on body size alone (Fleagle and Mittermeier 1980), by using bimanual locomotion and with the aid of their tails. In contrast, howlers (which travel mostly quadrupedally and are roughly of the same size as spider monkeys) use one large support at a time (Fleagle and Mittermeier 1980). Brachiation and climbing are likely to allow spider monkeys to shorten pathways between or within feeding patches, and suspension would enhance their maneuverability on thin supports. A quadruped would have to follow branches that zig and zag (Grand 1984).

It is likely that the ancestor of atelines was quadrupedal and the ancestor of atelins a brachiator (Figure 6.4). We base this conclusion on the fact that howlers and ateline sister-groups are quadrupedal, and that all atelins are brachiators (see Rosenberger and Strier 1989 for a similar conclusion).

There is a general tendency for larger-bodied mammals to be more folivorous than smaller ones (see above). The atelines are the largest New World monkeys and some of them are the most folivorous. Larger monkeys have absolutely greater nutri-

tional requirements and therefore need to feed on highly abundant resources, such as leaves. On the other hand, leaves are low-quality foods that require longer digestion than other kinds of food. Gaulin (1979) suggested that the lower basal metabolic rates of larger animals permit low rates of digestion. Within atelines, however, the pattern is not so simple. For example, the woolly spider monkey and the mantled howler (*Alouatta palliata*) eat comparable amounts of fruit in two different geographical locations, but the woolly spider monkey is twice as frugivorous as the sympatric brown howler (*Alouatta fusca*) studied during the same period (Strier 1992).

In any habitat where they co-occur, howlers are always more folivorous than atelins. Howlers occur in sympatry with other atelines over most of their range, but even where they occur alone (e.g., northern Argentina), howlers are the most folivorous of all Atelinae, which suggests that their diet became established in evolutionary time, and is not a mere recent ecological condition.

The geographical distributions of spider and woolly spider monkeys are, for the most part, mutually exclusive (Hernández-Camacho and Cooper 1976). Terborgh (1983) noted that they both are present in some regions of Peru, but that they never occur in the exactly the same places; they are always at least a few kilometers apart. This was considered as a good example of competitive exclusion by Waser (1987). But spider and woolly spider monkeys are sympatric in some places in Colombia (Izawa 1975; Stevenson et al. 1991, 1994) and Peru (Herrera, unpubl. data, cited in Peres 1994).

Woolly monkeys (*L. lagothricha lugens*) and long-haired spider monkeys (*Ateles belzebuth*) occur in sympatry at La Macarena, Colombia (Stevenson et al. 1991). Few differences were found in the way these species exploited resources. However, spider monkeys fed heavily on fruits of *Jessenia* while this item was absent from the diet of woolly spider monkeys. In addition, woolly spider monkeys fed heavily on insects, while spider monkeys rarely consumed them; this is the only reported case of heavy insect consumption by *Lagothrix*. These two divergences could be interpreted as a mechanism by which woolly spider monkeys can survive in sympatry with spider monkeys, given that both otherwise have very similar diets and modes of exploiting resources. It remains to be seen whether this characteristic of *L. lagothricha lugens* is an opportunistic strategy to overcome a presumed shortage of fruits, or is a fixed feature of this subspecies that occurs regardless of the availability of its preferred food.

Chapman (1987, 1988) studied the black-handed spider monkey, the mantled howler, and the white-throated capuchin (*Ateles geoffroyi, Alouatta palliata,* and *Cebus capucinus* respectively) in sympatry in Costa Rica over two years. Their diets showed high variability and overlap, leading him to conclude that it was unlikely that these species' diets could be influenced by interspecific competition (Chapman 1987). Tomblin and Cranford (1994) studied the white-throated capuchin (*Cebus capucinus*) and the mantled howler (*A. palliata*) elsewhere in Costa Rica, and reported that the two species used the same macrohabitats. However, based on a detailed study of branch use, feeding mode, positional behavior, and diet, they found significant differences between the species, at least during the rainy season. Even when both monkeys used exactly the same tree species at different times, they did not use them in the same way. The relative diameter of the branches used differed significantly, as did the distance from the trunk at which they foraged. Mantled howlers were concentrated on the periphery of the crowns, where they could reach the leaves, whereas capuchins showed a greater variability of branch use, spending part of the time on the periphery and also near the trunk. Capuchins ate a greater variety of food; the major components were fruit (44%) and invertebrates (37%), whereas the howlers were never observed eating fruit but instead ate leaves (94%) and buds (5.8%). Only howlers used their prehensile tail while feeding to suspend themselves near the tips of the branches.

In summary, atelines seem to have acquired key innovations in a stepwise fashion: all of them share a prehensile tail and suspensory positional behavior. A nested subset of atelines – the spider, woolly, and woolly spider monkeys – have developed the ability to travel bimanually. Field observations suggest that tail prehensility opens access to many resources that would be otherwise inaccessible.

Pithecinae

Pithecins possess unique dental characteristics that allow exploitation of resources that other species do not exploit. They have sharp canines which they use to open hard-husked, immature fruits. Bearded sakis possess the most remarkable canines with which they can open the hardest fruits (Kinzey and Norconk 1993). Living pithecins have very procumbent upper incisors (an unknown character in *Cebupithecia*), which they use to open some kinds of fruits (van Roosmalen et al. 1988).

In addition to sharp canines and procumbent incisors, living pithecins share a thin crenulated molar enamel and reduction in molar relief. Pithecins break the husk of some fruits and masticate the seeds inside. These seeds are usually softer than seeds of fruits that do not possess a hard husk and are usually swallowed and dispersed undigested. Low occlusal relief may resist wear well (Rosenberger and Kinzey 1976). The absence of a thick enamel could be correlated with the consistency of seeds: they may be hard to masticate, but they are not brittle (Kinzey 1992). The fossil pithecin *Cebupithecia sarmientoi* seems to be the sister-group to recent pithecins. It displays long sharp canines, similar in shape to those of living pithecins, but the molars have a higher relief and the enamel is not crenulated. This suggests a two-stage evolution of sclerocarpic foraging in pithecins: the characters that enabled them to open fruits arose first, and then molar modifications evolved which were (presumably) advantageous for seed processing; the latter modifications are seen in recent forms only (Setoguchi et al. 1988; Kinzey 1992). As in the atelines, key characters in the pithecines appear to have evolved in steps, not as an integrated complex.

Uakaris and bearded sakis seem unlikely to be sympatric because both are frugivores specialized in seed consumption (Ayres 1989). Sakis and bearded sakis also have similar diets, yet they co-occur throughout most of their geographical range (Kinzey and Norconk 1993). Some differences have been noticed in behavior that might partly explain their capacity to share the same habitats. Guianan sakis tend to forage in lower levels of the canopy (van Roosmalen et al. 1988; Mittermeier and van Roosmalen 1981) and eat softer pericarps (Kinzey and Norconk 1993) than sympatric

bearded sakis. Sakis also eat more flowers during the dry season, when fruit avail-
ability is depressed, while bearded sakis continue to specialize on fruits (Kinzey and
Norconk 1993).

The geographic distribution of spider monkeys also overlaps extensively with
those of sakis and bearded sakis. Like bearded sakis, spider monkeys are upper-
canopy frugivores (Norconk and Kinzey 1994). Sakis that feed in the understory and
lower canopy use different plant species (van Roosmalen et al. 1988). Fruits represent
over 90% of the diet of both the black spider monkey (*Ateles paniscus*) and the black
bearded saki (*Chiropotes satanas*) and their diets overlap in a number of species. The
bearded saki exploits many fruits at an earlier stage than the spider monkey, when
they are still unripe and much harder to open. The bearded saki opens fruits signifi-
cantly harder than those the spider monkey does, whereas the average hardness of
the fruits sakis open is intermediate and not significantly different from the other two
taxa (Kinzey and Norconk 1990; 1993). Species of sakis and bearded sakis that do not
overlap in distribution have more similar ecological characteristics (Peres 1993).
Given all factors described above, there is no strong evidence of an evolutionary
divergence in the ecology of sakis and bearded sakis, at least at a broad generic level.

In Venezuela, the diets of the black bearded saki (*Chiropotes satanas*), black spider
monkey (*Ateles paniscus*), and long-haired spider monkey (*A. belzebuth*) have been
studied in sympatry (Kinzey and Norconk 1990; Norconk and Kinzey 1994) and
allopatry (Kinzey and Norconk 1993). Although the data available are limited, they
give no indication of competitive release (Norconk and Kinzey 1994). This suggests
that while sakis and spider monkeys overlap in food sources, they may not compete
with each other intensively.

At least one species of titi monkey (*Callicebus brunneus*) has been reported to
include immature fruits in its diet, as do pithecins (Wright 1989). The yellow-handed
titi monkey (*C. torquatus*) opens most hard fruits with its canines (as do pithecins) or
premolars (Kinzey 1977a), in contrast with capuchins that open hard fruits with pre-
molars or molars (Janson and Boinski 1992). This habit of titi monkeys of using their
canines to open fruits could be the beginning of a tendency in the clade, despite the
fact that titi monkeys have the relatively smallest canines among living platyrrhines.
They also share lower molars (especially the second) that show a subequal height of
trigonid and talonid with the other pithecines. This character could have some rela-
tion with reduction of occlusal relief and mastication of seed and as pointed out for
pithecins (Rosenberger and Kinzey 1976) but this is not possible to test at the moment.
There are no reports of seed-predation in titi monkeys.

A few subspecies of titi monkeys overlap in their geographical distributions: *C.
torquatus torquatus* overlaps with both *C. cupreus discolor* and *C. c. cupreus* in Peru and
western Brazil (Soini 1972; Kinzey 1978; nomenclature follows Mittermeier et al.
1988); *C. cupreus* and *C. torquatus* also have been reported to overlap in southern
Colombia (Hernández-Camacho and Cooper 1976; Klein and Klein 1976). But geo-
graphical overlap does not imply spatial co-occurrence: different habitat preferences
were detected, at least for *C. t. torquatus* and *C. c. discolor* (Soini 1972; Moynihan 1976a;
Kinzey 1978, 1981; Kinzey and Gentry 1979). These studies also found interspecific

differences in dental morphology, diet, and preferences in canopy levels, among other
factors (Kinzey 1978). These data suggest an adaptive radiation at the species level.

To summarize, Pithecinae are characterized by a few morphological characters, of
which none can be identified as a key innovation at present. In contrast, Pithecini is
supported by a suite of dental characters (e.g., sharp canines) that can be considered
key innovations. In addition, living pithecins show low cusp relief. The evolution of
these characters in two steps suggests that ability to open hard-husked fruits and mas-
ticate the enclosed seeds evolved in separate phases. This is another example of evo-
lution in steps through key innovations. Within living pithecins, uakaris show the
most remarkable divergence in that they specialize in living in flooded forests.

Cebidae

AOTUS – Owl monkeys bear several traits that may represent key innovations for
a nocturnal habit. They have the lowest metabolic rate among the few known for
platyrrhines (Le Maho et al. 1981). All nocturnal primates have low metabolic rates,
although this is not true for all nocturnal mammals (McNab 1983). Low metabolic
rates presumably allow nocturnal animals to live with much lower levels of energy
consumption (Crompton et al. 1978).

Owl monkeys have relatively larger eyes than other platyrrhines, which enhance
vision at low light levels. Its lens is more spherical than in diurnal forms, a shape that
refracts more light onto the retina (Wright 1989, 1994). The iris is located more pos-
teriorly, toward the center of the eye, allowing the pupil to reach a larger diameter
and more light to reach the retina (Noback 1975). In addition, according to Ogden
(1975), the rod density throughout the retina is several times higher than that of
humans. The size of the olfactory lobes of the brain relative to the size of the visual
cortex suggests that olfaction is more important in owl monkeys than in other
platyrrhines (Wright 1989).

SAIMIRI AND *CEBUS* – Differences in behavior seem to be the key to differential
resource exploitation in capuchins (*Cebus*) and squirrel monkeys (*Saimiri*) (Janson and
Boinski 1992). Certain behaviors are shared by these genera; an example is the manip-
ulative foraging through foliage and small twigs when searching for insects. But this
behavior is also displayed by callitrichins, their sister-group, and so appears to be a
primitive condition for *Cebus-Saimiri*.

Body size and biting force may permit capuchins to forage in hidden, mechani-
cally tough substrates, such as palm frond bases, cane, bamboo, dead branches, and
termite nests (Janson and Boinski 1992); the most robust species (*Cebus apella*) spends
up to 44.3% of its time associated with such substrates (Terborgh 1983). By compari-
son, squirrel monkeys spend only 0.7% of their time searching in such difficult sub-
strates. Capuchins (especially *C. apella*) also possess very thick dental enamel, rela-
tively more substantial than that in any other living primate (Kay 1981). This may be
related to the fact that they feed on very hard plant tissues, such as palm nuts (Izawa
and Mizano 1977).

As mentioned earlier, capuchins provide one of the few cases of congeneric sym-
patry in New World monkeys. This raises the question of whether differences in the

way the sympatric capuchins exploit the environment suggest an adaptive radiation within the genus. The tufted capuchin (*C. apella*) and white-fronted capuchin (*C. albifrons*) have been studied in sympatry in Manú National Park in Peru (Terborgh 1983; Janson 1985; Janson and Boinski 1992). These species showed some differences in their dietary preferences: the tufted capuchin was seen more frequently foraging on figs; the white-fronted capuchin, on palm trees. The tufted capuchin showed an ability to break palm nuts not seen in the white-fronted capuchin; the latter always took much longer to break such nuts. The tufted capuchin forages heavily on palm nuts in other parts of its geographical distribution where it is not sympatric with the white-fronted capuchin, such as northeastern Argentina (I. Horovitz, pers. obs.); therefore, this dietary trait does not seem to be a localized specialization of the Manú population, but more likely is a characteristic of the species.

There are also some morphological differences between these two capuchin species. The tufted capuchin has a larger body weight and is therefore stronger; it also has a deeper and more buttressed mandible, larger zygomatic arches, and some individuals possess a sagittal crest, all suggesting a larger biting force. These characters are consistent with the tufted capuchin's frequent habit of breaking dead branches in search of insects and the use of palm nuts as a common food source (Terborgh 1983; Janson 1985; Janson and Boinski 1992).

All capuchin species have an ability to exploit a wide range of food items. This may be derived from their ability to manipulate substrates and employ tools, abilities not possessed by other New World primates (Costello and Fragaszy 1988; Chevalier-Skolnikoff 1989a; Fragaszy et al. 1990; Visalberghi 1990). An animal uses a tool when it employs an unattached environmental object as a functional extension of its own body in attaining an immediate goal (van Lawick-Goodall 1970). Sensorimotor ability, tool use, and omnivorous extractive foraging have a morphological correlate: brain size (Gibson 1986; Janson and Boinski 1992). When seasonal sources are scarce in the low season, capuchins can extract embedded food which is available year-round and has high concentrations of energy and protein (Parker and Gibson 1977). This might be the reason why capuchins can inhabit areas not inhabited by other monkeys that do not have the ability to engage in extractive tasks involving complex, cortically mediated, sensorimotor coordinations for tapping, probing, looking, and listening to locate and recognize bark-embedded insects, ripe palm nuts, frogs, and grasshoppers hidden within tree cavities (Izawa and Mizano 1977; Izawa 1978, 1979a; Terborgh 1983; Gibson 1986). Most studies on tool-use in capuchins have been conducted with captive individuals. In the wild, capuchins have been observed to use sticks as probes and clubs (Boinski 1988; Chevalier-Skolnikoff 1989b), and to employ oyster shells as hammers (Fernandes 1991) although these events are quite rare. They frequently open nuts and other hard fruits by pounding them against tree trunks or by hitting them together (Izawa and Mizano 1977). Tool-use is typical of animals who lack specialized anatomical characteristics and need to extract embedded food (Alcock 1972; Gibson 1986). Extraction *per se* is not correlated with brain size. Extractors who possess a rather specialized anatomy to concentrate on one extractive food (such as the marmosets), tend to have small brain sizes relative to body size (Gibson 1986).

CALLITRICHINI – Claws in this group serve a vital function, allowing individuals to cling to trunks and other vertical supports while exploiting plant exudates and insects, and/or to leap from trunk to trunk as a traveling behavior (Cartmill 1974; Garber 1980, 1992; Rylands and de Faria 1993). Such supports are too large for small primates to span with tiny hands and feet; therefore, the possession of claws seems a character required for clinging onto trunks. Two hypotheses have been suggested for the original function of claws in the Callitrichini, involving either feeding on tree exudates (Sussman and Kinzey 1984) or traveling on large supports (Ford 1986a). Two hypotheses have been suggested for the original function of claws in the Callitrichini, involving either feeding on tree exudates (Sussman and Kinzey 1984) or traveling on large supports (Ford 1986a). To test these two hypotheses we need to assume that feeding and traveling behaviors shown by each species are genetically fixed.

All callitrichins studied in the wild feed on exudates, with the apparent exception of Goeldi's monkey (Sussman and Kinzey 1984; Garber 1992). Ford (1986a) based the second hypothesis on the observation that Goeldi's monkey (which she considered basal to callitrichins) uses its claws to travel by vertical clinging and leaping. Other species that can be characterized as using a clinging-and-leaping mode of progression are *Saguinus fuscicollis*, and *Cebuella pygmaea* (Kinzey et al. 1975; Moynihan 1976b; Castro and Soini 1977; Sussman and Kinzey 1984). Even so, *Saguinus* and *Cebuella* use their claws primarily for clinging to vertical supports while feeding on exudates rather than for locomotor activities (Kinzey et al. 1975; Sussman and Kinzey 1984). Some species rarely cling onto trunks to forage for insects (*Saguinus mystax* and *S. geoffroyi* [Garber 1992]). The answer to whether Goeldi's monkey lost the habit of feeding on exudates, or most other species virtually abandoned the habit of clinging and leaping and hence the use of their claws while traveling, would be not much more than a guess at this point. If Goeldi's monkey were sister to the marmosets (*Callithrix-Cebuella*), then the travel hypothesis for origin of claws would be even less likely. On this basis, we infer that Goeldi's monkey lost its habit of feeding on exudates secondarily.

Callitrichins share an ability to search for hidden insects with capuchins and squirrel monkeys; therefore, it seems likely that this ability evolved in their common ancestor. All species of lion tamarins (*Leontopithecus*) also have the ability to search for embedded insects.

The variety of environments and resources callitrichins exploit are not restricted to individual clades. Species belonging to different genera have converged in their ecological characteristics. There is only one strong tendency that marmosets exhibit which is not found in other groups: the most specialized form of exudativory, evidenced by their habits and morphology.

The geographic distributions of congeneric callitrichine species and subspecies are generally non-overlapping. Where sympatry does occur, there is a relatively sharp differentiation in the way the different types exploit the environment (Ferrari 1993). The saddle-back tamarin (*Saguinus fuscicollis*) is sympatric over part of its distribution with marmosets and some of its congeners. It appears to capture larger prey than its sympatric congeners by foraging in specific sites such as holes and fissures in bark

and leaf litter accumulations (Yoneda 1981, 1984; Terborgh 1983), in contrast with the less manipulative techniques of "scan-and-pounce" or leaf-gleaning used by other species. Another important difference is that saddle-back tamarins typically forage at lower levels in the forest than its congeners; this difference persists even in the absence of other callitrichins (Pook and Pook 1981; Terborgh 1983; Yoneda 1984; Soini 1987; Buchanan-Smith 1990; Fang 1990; Heymann 1990; Ferrari 1993). The two smallest tamarin species – the saddle-back tamarin (*S. fuscicollis*) and the black-and-red tamarins (*S. nigricollis*) – forage in the lowest forest strata (< 11 m height), while the larger species occupy mostly the middle strata and lower parts of the main canopy (> 10 m height) (see Soini 1987). We regard this as a genetically fixed preference; it is possible that it facilitates the coexistence of *S. fuscicollis* and other callitrichins.

Possession of claws and a small body enable callitrichins to feed and travel in lower forest, on substrates that may be inaccessible to other monkeys. Claws seem to have been a key innovation that paved the way for further specializations in the marmosets, including modified canines and incisors. This seems to be a case of progressive specialization for a new niche: exploitation of plant exudates. Goeldi's monkey, the putative sister-group of the marmosets, has lost the habit of exudate-feeding and many of the morphological characteristics inferred to occur in their common ancestor.

All cebids are strongly insectivorous, but their searching strategies vary. Owl monkeys look only for insects exposed on the surface of the branches or in the air. In contrast, capuchins, squirrel monkeys, and callitrichins have evolved manipulative abilities and search for insects hidden under leaves, or (in *Cebus* and *Leontopithecus*) for insects under bark. Did such manipulative abilities evolve more than once in the New World monkeys? According to the currently most parsimonious scenario – in which capuchins, squirrel monkeys, and callithrichins form a monophyletic group (Figures 6.3 and 6.4) – manipulative abilities appear to have evolved only once. However, given that the monophyly of this group is weakly supported, this conclusion should be considered provisional.

Conclusions

We conducted a "total evidence" analysis for New World monkeys at the generic level, combining nuclear and mitochondrial DNA sequences and morphological characters. The tree obtained is congruent with that derived excluding morphology. The New World monkeys appear to have undergone a basal split into two clades: Atelidae = (Atelinae, [*Callicebus*, Pithecini]) and Cebidae = (*Aotus*, [{*Cebus*, *Saimiri*}, Callitrichini]). Neither of these clades seems to display marked morphological "key innovations" – that is, synapomorphies that allow them to exploit resources in a specialized fashion. However, both show an evident difference in ecology: Atelidae are mainly herbivorous, whereas Cebidae have a heavy component of insectivory. The only clades unsupported by morphological characters are (*Brachyteles*, *Lagothrix*) and the two most basal nodes of (*Saguinus*, [*Callimico*, {*Callithrix*, *Cebuella*}]).

Owl monkeys (*Aotus*) appear to be sister to the remaining cebids, all of which have a strong component of insectivory. While owl monkeys only search for insects exposed on the surface of the branches or in the air, their sister taxon has evolved manipulative abilities and search for hidden insects and, in some cases, embedded ones. This basal position of *Aotus* is, however, only two steps more parsimonious than alternative topologies (see above), so we consider the conclusions based on this apparent position to be tentative.

Atelines display a prehensile tail and suspensory positional behavior, and the atelin subclade has developed the ability to travel bimanually. These seem to be key innovations for access to and exploitation of certain food resources, particularly fruits and leaves near branch tips. Pithecins possess sharp canines; a nested subset of this group shows low cusp relief, which may be important in the exploitation of hard-husked fruits and mastication of seeds. Possession of claws and small body size may enable callitrichins to feed and travel in the lower strata of rain forests. Claws may also have been a prerequisite for dental adaptations for exploiting plant exudates in marmosets.

In each of the three clades just mentioned, batteries of morphological characters appear to perform specific functions in an integrated fashion. Our phylogenetic analysis shows these batteries appear to have evolved in a stepwise fashion – that is, early diverging taxa possess only one or some of these derived characters, while more derived groups show more of these characters. It appears that these characters often serve the same functions in both basal and derived groups, although in some cases additional functions are observed in the latter. Major morphological characters seem important in several nodes, because they appear associated with the exploitation of new resources. Most ecological studies of New World primates focus on differences between co-occurring species in their use of resources. Given that, at least in some cases, such differences persist in allopatry as well and are somewhat characteristic of the species involved, it appears that most of the ecological variations in this group do in fact represent evolutionary trends. Differentiation in behavior also seems to be important at or below the generic level, and does not always have obvious morphological correlates; inclusion of such behavioral differences promises to be an important new direction for research on the adaptive radiation of the New World monkeys.

Acknowledgments

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