

# New World Monkeys

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**New World monkeys are the nonhuman primates of South and Central America. Because almost all of their evolutionary history took place on the island continent of South America without competition from other primates, and most likely in a strictly arboreal setting, the character of their adaptation is unique. Fossils and molecules indicate the major lineages are long enduring, having attained diverse, stable ecological conditions quite early. Today, platyrrhine (wide-nosed) monkeys comprise the most diversified taxonomic group among anthropoids. More primitive anatomically than Old World monkeys or apes, some forms resemble early fossil anthropoids from Egypt and serve well as models for reconstructing their behaviour. Others are more like the specialised apes in their locomotor adaptations, or the modified, folivorous leaf monkeys, whereas some evoke the big-brained, extractive foraging strategies of African apes. Highly varied in their outward appearance as well, the range of social behaviours and mating strategies exhibited by platyrrhines is without equal among the primates.**

## Introduction

New World monkeys are found in wooded habitats from southern Mexico to northern Argentina and everywhere are threatened with extinction. They have differentiated into a wide variety of microhabitats and foraging niches in northern neotropical ecosystems, including the extensive networks of gallery forests that spread from the Amazon basin into savannah-like grasslands. Scientists recognise 16 different genera of living New World monkeys and more than two dozen extinct genera ranging back in time to approximately 26 million years ago (Ma) (Table 1 and

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## Introductory article

### Article Contents

- Introduction
- Basic Design
- Diversity
- Habitats and Abundance
- Habits and Life Histories
- Fossil History
- Phylogeny

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Table 2). A splinter radiation, only recently extinct, inhabited the Greater Antilles in the Caribbean Sea, and early members of the group are found at fossil sites in Patagonia, near the southern tip of South America not far from the Antarctic Peninsula.

## Basic Design

New World monkeys (Figure 1) are anthropoid primates. The formal term for the group is Infraorder Platyrrhini, which refers to the broad, flat shape of their external nose, with nostrils set wide apart. It contrasts with Catarrhini, which refers to the Old World monkeys, apes and humans. They have a narrow nose with close-set nostrils. By tradition, platyrrhines are also distinguished from other living monkeys and apes by such features as three premolar teeth instead of two in each toothrow, and an eardrum that is placed near the sidewall of the skull and framed by a flattened C-shaped band of bone, as opposed to one that is set more deeply in the head, at the inner edge of a bony tube that extends to the side. But the more important distinction is phylogenetic. Platyrrhines, while anthropoids, are actually only distant relatives of the Old World cercopithecoid monkeys. Even though the word 'monkey' is used in referring to both groups, this expression has come to be a customary term of art. Old World monkeys are actually more closely related to apes (hominoids) than they are to New World monkeys.

Knowing that imparts more significance to the contrasting snouts of platyrrhines and catarrhines than the presence or absence of a pug nose muzzle. For platyrrhine noses also resemble the wide noses of tarsiers, an east Asian primate that represents a very early branch of the larger taxonomic group to which anthropoids belong, called Haplorhini. This suggests that catarrhine noses are a specialised variety, having evolved their shape from something resembling a platyrrhine nose. Although the reasons for this are not at all understood, it may explain something inherent in the earliest anthropoid skulls known, which have wide nasal bones and a broad nasal opening – they looked like platyrrhines. And, this turns out to be a much broader theme that contextualises how living platyrrhines and catarrhine are positioned relative to one another in

**Table 1** Genus level classification of living New World monkeys

Family	Subfamily	Genus	Common name	Number of species
Atelidae	Atelinae	<i>Ateles</i>	Spider monkey	4
		<i>Alouatta</i>	Howler monkey	7
		<i>Lagothrix</i>	Woolly monkey	2
		<i>Brachyteles</i>	Woolly spider monkey	1
Pitheciidae	Pitheciinae	<i>Pithecia</i>	Saki	5
		<i>Chiropotes</i>	Bearded saki	2
		<i>Cacajao</i>	Uakari	2
	Homunculinae	<i>Aotus</i>	Owl monkey	9
		<i>Callicebus</i>	Titi monkey	10
Cebidae	Cebinae	<i>Cebus</i>	Capuchin	4
		<i>Saimiri</i>	Squirrel monkey	4
	Callitrichinae	<i>Callithrix</i>	Marmoset	10
		<i>Saguinus</i>	Tamarin	12
		<i>Leontopithecus</i>	Lion tamarin	3
		<i>Callimico</i>	Goeldi's monkey	1
		<i>Cebuella</i>	Pygmy marmoset	1

primate evolution. Platyrrhines tend to be the more primitive ones.

There are other measures indicative of the distance between the so-called monkeys and the profound separation of modern platyrrhines and catarrhines. The three-premolar dental formula and the nontubular ectotympanic bone of platyrrhines are primitive retentions as well, meaning they are holdovers of deep-rooted features lost in cercopithecoids and apes but widespread among the archaic anthropoids they replaced. These include genera such as *Parapithecus* and *Apidium* (both with wide noses) from late Eocene and Oligocene beds of the Fayum deposits of Egypt (Seiffert *et al.*, 2010). Although no platyrrhine fossils of comparable antiquity have yet been discovered, the comparative anatomical implications of extant morphology come as no surprise. New World monkeys, which began their evolution early in anthropoid history, exhibit suites of primitive features, like a rather small body size. Several platyrrhines, and a number of the New World fossils, weigh in at approximately 1000 g and the miniature marmosets and tamarins usually weigh no more than 500 g. This, again, compares favourably with primitive anthropoids from the Fayum (Fleagle, 1999). At the other end of the spectrum, the largest living platyrrhine is no larger than the 10 000 g miqui. However, it is also known that some extinct Pleistocene species were more than twice that size, which raises another issue, the possibility that we have been wrong to think that body size evolution among platyrrhines has been somehow constrained in ways that did not limit catarrhines. Weighing approximately 20 kg, these two species may be gigantic for platyrrhines, but they are hardly impressive as far as the

bigger Old World monkeys and apes are concerned. **See also:** [Old World Monkeys](#); [Primates \(Lemurs, Lorises, Tarsiers, Monkeys and Apes\)](#)

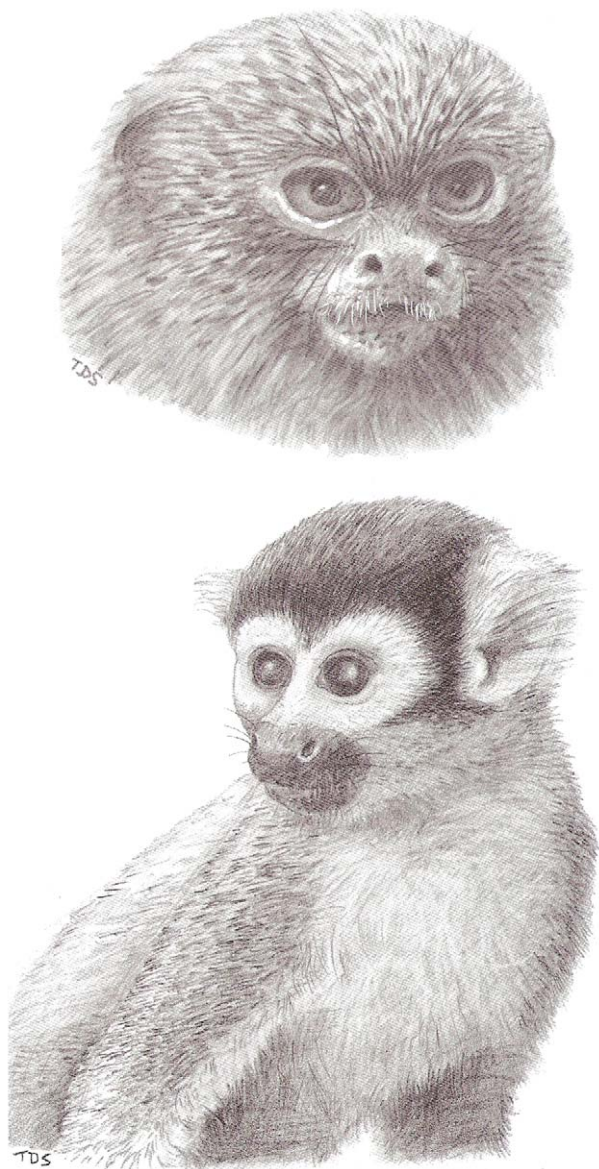
As a corollary to the New World monkeys being the smallest living anthropoid primates, they are also the most exclusively arboreal and a corollary to that lifestyle is the exceptional variety of ecological adaptations that have evolved among them. No genus uses the ground frequently or consistently across its geographic range, although many are competent when venturing out from the trees to cross open patches of landscape, escape injury, engage in play or forage briefly in the litter below. In the trees, they practise a wide variety of locomotor or positional behaviours, more like the Old World strepsirhines than the narrowly adapted catarrhine monkeys. General anatomical features associated with arboreal quadrupedalism are accentuated by two strategic adaptive extremes, the smaller marmosets and tamarins where vertical clinging and leaping from support to support and below the canopy is advantageous, and the larger prehensile-tailed atelid monkeys, where long-limbed climbing, suspension and brachiation are emphasised (Youlatos and Meldrum, 2011). The locomotion of marmosets and tamarins, which involves a secondary evolution (sometimes called a reversal) of claws on all digits except the big toe (Maiolino *et al.*, 2011), is a consequence of body size reduction, not primitiveness. Marmosets and tamarins are thus important examples of 'dwarfism', a derived adaptive package that has involved changes in dentition and reproduction as well as locomotion. Their clawed locomotor pattern is also the best available living analogue among primates for the postural and locomotor behaviour of the earliest members of the order, the primitive

**Table 2** Chronology, geography and taxonomy of the platyrrhine fossil record

Geological age	Locality	Taxon	Key specimens	Affinities
Late Oligocene≈26 Ma	Salla, Bolivia	<i>Branisella boliviana</i>	Jaw fragments	??
Early Miocene≈20 Ma	Central Argentina	<i>Szalatavus attricuspis</i> <i>Dolichocebus gaimanensis</i>	Jaw fragments Cranium	?? Squirrel monkeys (?)
	Central Argentina	<i>Tremacebus harringtoni</i>	Cranium	Owl monkeys
	Central Chile	<i>Chilecebus carrascoensis</i>	Dentition	Cebines
Middle Miocene≈17 Ma	Central Argentina Patagonia	<i>Mazonicebus Soriacebus</i> spp.	Dentition	Pitheciines
	Patagonia Patagonia	<i>Carlocebus</i> spp. <i>Homunculus patagonicus</i>	Dentition Partial skeleton	Pitheciines Pitheciines
Middle Miocene≈16 Ma	Central Argentina	<i>Proteropithecina neuquensis</i>	Dentition	Pitheciines
Middle Miocene≈11–14 Ma	La Venta, Colombia	<i>Stirtonia</i> spp.	Dentition	Howler monkeys
		<i>Neosaimiri fieldsi</i>	Dentition	Squirrel monkeys
		<i>Laventiana annectens</i>	Dentition	Cebines
		<i>Cebupithecina sarmientoi</i>	Partial skeleton	Pitheciines
		<i>Nuciraptor rubricae</i>	Dentition	Pitheciines
		<i>Miocallicebus</i>	Dentition	Titi monkeys
		<i>Mohanamico hershkovitzi</i>	Dentition	Callitrichines
		<i>Aotus dindensis</i>	Dentition	Owl monkeys
		<i>Lagonimico conclutatus</i>	Crushed skull	Pitheciines
		<i>Patasola magdalena</i>	Dentition	Callitrichines
		<i>Micodon kiotensis</i>	Isolated teeth	Callitrichines
		<i>Acrecebus fraileyi</i>	Isolated tooth	Cebine
		Middle Miocene≈8 Ma	Acre, Brazil	<i>Solimoea acensis</i>
<i>Protopithecus brasiliensis</i>	Complete skeleton			Howler monkeys
Pleistocene < 500 000 BP	Bahia, Brazil	<i>Caipora bambuiorum</i>	Complete skeleton	Spider monkeys
		<i>Xenothrix mcgregori</i>	Cranium, mandible	Pitheciines
Holocene≈3000–7000 BP	Jamaica	<i>Antillothrix bernensis</i>	Dentition	Pitheciines
	Dominican Republic Haiti	<i>Insulacebus toussaintiana</i>	Dentition	Owl monkeys (?)
	Cuba	<i>Paralouatta varonai</i>	Cranium, mandible	Howler monkeys

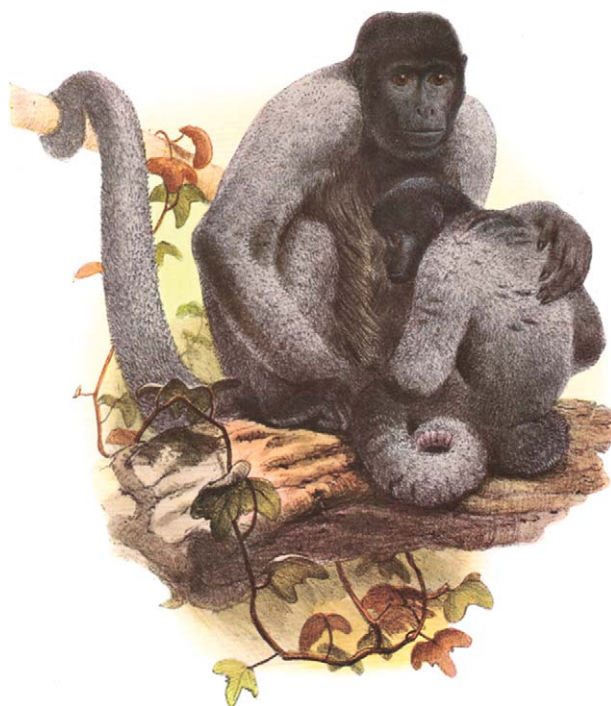
plesiadapiforms, a group that had clawed digits, too. In contrast, the climbing-based quadrupedalism of atelids, which include the spider (*Ateles*) and woolly (*Lagothrix*) monkeys (Figure 2), parallels the arboreal manner of apes in a general way but with the added twist of having a grasping tail – almost a fifth limb – which is used in suspended postures as well as brachiating locomotion. Tail prehensibility has actually evolved twice among platyrrhines

(Rosenberger, 1983), once in the last common ancestor of atelids and once in the capuchin monkey (*Cebus*) lineage. In the latter case, the tail is often called semiprehensile as it lacks several features shared by the atelids that are suited to highly dynamic tail use as opposed to the more static applications of capuchins (Organ *et al.*, 2011). These include the atelid's greater relative tail length, a finger-like pad of sensitive friction skin on the underside near the tail's



**Figure 1** Portraits of the pygmy marmoset (*Cebuella*), top, and the squirrel monkey (*Saimiri*), two New World monkeys belonging to the frugivorous–insectivorous cebid clade. Original artwork by Timothy D Smith.

end that is particularly sensitive to heavy-pressure touch, specialised musculoskeletal arrangement designed to facilitate twisting and coiling and an unusual expansion of the area of the brain relating to the tail's motor control. Another unique lifestyle involving a different adaptive dimension, when activity takes place, concerns the owl monkey *Aotus*, the only nocturnal anthropoid. These individual departures from a conservative but flexible anthropoid body plan and daily routine reflect the multiple ways New World monkeys have come to adapt not only to habitat and food types, but also to the need to partition resources among potential competitors, meaning all the

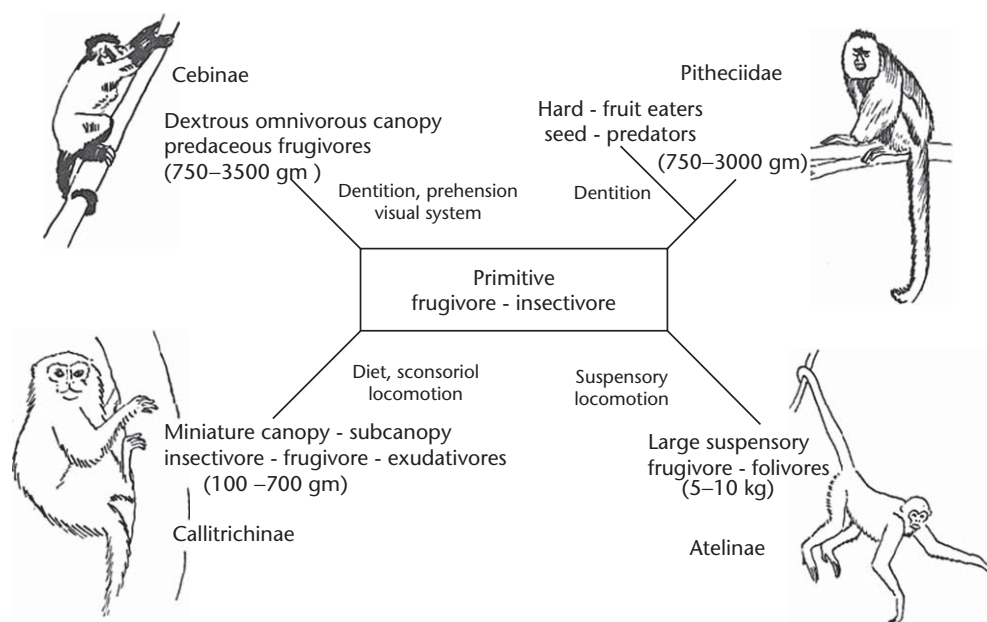


**Figure 2** Portrait of one of the prehensile-tailed New World monkeys, the woolly monkey (*Lagothrix*). Grasping tails evolved twice among platyrrhines, once among early atelids, as represented here, and once in a cebid, the capuchin monkey (*Cebus*). The capuchin tail is often called semiprehensile as it lacks several features shared by the atelids, including great length, a finger-like pad of sensitive friction skin on the underside near the tail's end, and an unusual expansion of the area of the brain relating to its motor control. From Elliot (1913). © American Museum of Natural History.

local primates which occupy the diverse ecological communities present in tropical forests of Central and South America.

## Diversity

As with other primates, the taxonomy of New World monkeys has become quite unstable in recent years as systematists grapple with the need for a consistent vocabulary, a bounty of molecular studies that have added an additional perspective on phylogenetics to the more traditional morphology (Wildman *et al.*, 2009), changing views of the species concept and the legislative needs of the conservation movement's dialogue with governments, which prefer to focus on preserving species as opposed to ecosystems (Rosenberger, 2012). A conservative classification of the living platyrrhines recognises 16 genera and approximately 75 species, although the latter figure may be half the number often cited in reviews. The modern classification above the genus level is robust, however, for it is based on the concordance of morphology and molecules (Schneider and Rosenberger, 1996), the outlines of which have been confirmed by many studies. Four major



**Figure 3** An ecophylogenetic model of the New World monkey adaptive radiation. The four major taxonomic clades occupy semi-discrete adaptive zones. Each is distinguished primarily by a discrete combination of dietary and locomotor adaptations, as well as body mass, that evolved from a more primitive, generalised ancestor. Reused from Rosenberger (2011).

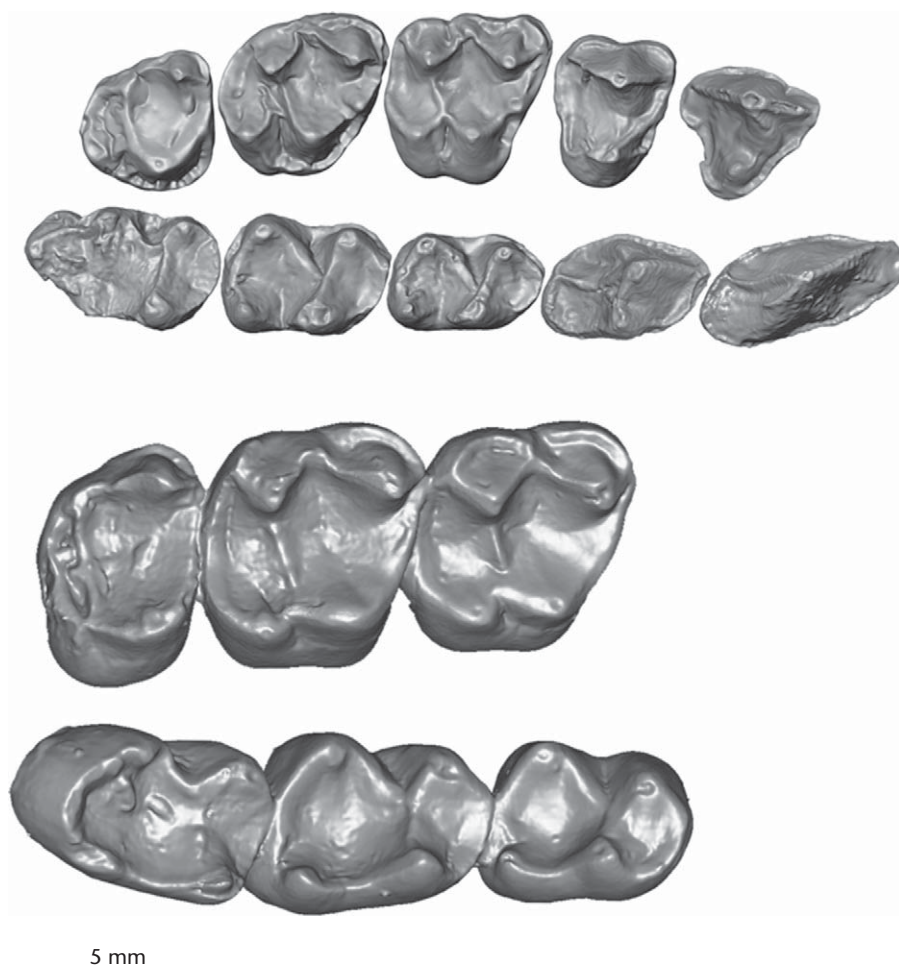
subfamily radiations (Figure 3), in three families, are indicated (Table 1). This quartet is a widely accepted arrangement although it is troubled by one exception, the genus *Aotus*. Its placement continues to be debated, for the morphological and molecular signals of relatedness appear to be at odds (Rosenberger and Tejedor, in press; Perez *et al.*, 2012). Morphologists tend to interpret *Aotus* as a close relative of the titi monkey (*Callicebus*), within Family Pitheciidae, whereas molecular studies consistently place it in an entirely different clade, Family Cebidae. **See also:** [Classification](#)

## Habitats and Abundance

New World monkeys live most densely in arboreal habitats throughout the Amazon basin, the world's richest land-based ecosystems. Taking advantage of the profusion and variety of edible plant parts and the animals that live in trees (mostly insects, arthropods and small vertebrates), platyrrhines have evolved a broad spectrum of niches by adapting to different food sources concentrated in different areas of the forest canopy and subcanopy, as well as the seasonal timing cycles of bloom and bust that drive the availability of food. Thus, it is not unusual for a dozen monkey species to share the natural stores of a particular area without directly competing for any one crucial resource: the large howler monkeys may forage for leaves and fruits at the uppermost levels of the canopy as the small marmosets and tamarins, taking advantage of their specialised clawed fingertips, cling and leap among the large calibre trunks and lianas of the

lower canopy, scrounging for insects and gums; the saki monkeys split open woody legumes to extract seeds as the spider monkeys rely on soft fruit and the capuchins eat palm nuts. When their favourite items are depleted during the dry season, the animals switch their foraging behaviours to an alternate strategy that continues to keep their niches sufficiently separate. This variety in foraging and feeding makes the platyrrhine a very useful source of analogies in reconstructing the behaviour and adaptations of extinct primate species (Figure 4). The built-in-flexibility that corresponds with these arboreal methods has enabled some platyrrhines to expand geographically along treed watercourses into the drier woodlands outside of Amazonia. But the contrast in what these different habitats can support is dramatic. One may find a dozen monkey species occupying the same general vicinity in Amazonia but in the gallery forests five very different species coexisting would be the maximum.

From another perspective, few actual populations of New World monkeys are considered abundant, and several species face imminent extinction. The miqui, or woolly spider monkey, and the lion tamarin, both located only in the imperilled Atlantic Coastal Forest of eastern Brazil, are perhaps the most endangered. That tropical rainforest, which is separate from Amazonia and composed of its own distinctive ensemble of flora and fauna, has been decimated since Europeans arrived approximately 500 years ago. The survival of these and many other New World monkey species into the twenty-first century will require an aggressive conservation and education programme to secure the future of the few forest tracts where they remain (Strier, 2011).



**Figure 4** An example of how the diverse adaptations of platyrrhine contributes to understanding parallel evolution and reconstructing the behaviour of fossils. Cheek teeth (1st–3rd molars) of the semifolivorous howler monkey (bottom rows, uppers above and lowers below), *Alouatta*, shows a remarkable resemblance to a fossil from the Fayum, Egypt and *Afradapis* that is related to early members of the strepsirhine (lemurs and lorises) group. *Afradapis* courtesy of Erik Seiffert. Reproduced from Rosenberger *et al.* (2011b).

## Habits and Life Histories

New World monkeys are typical primates in the sense that they eat a wide variety of things, may congregate in relatively large groups, have small litters of no more than one offspring or two (in marmosets and tamarins) and long lactation periods, and they grow up and develop in a context that emphasises learned behaviour. As an overall pattern, platyrrhines, like many other primates, balance their diets by combining a core staple of fruits for carbohydrates, fats and sugars with a variety of alternative sources of protein, which usually comes from prey, leaves or seeds depending on body size, gut specialisations, special features of the dentition and other foraging adaptations. However, among them there are dietary specialists: leaf-eating in the case of the howler monkeys, ripe fruit in the spider monkeys, tree gum in the marmosets, the seeds or pulp of hard-shelled fruits like legumes in the saki and uakari monkeys, and in cebus monkeys – a predaceous,

frugivorous omnivore – sheer eclecticism predicated on relatively large brains, physical strength and excellent manual dexterity. *Cebus* monkey feeding, in fact, can be an awe-inspiring event. Like chimpanzees, they will pound a hard nut against a stone anvil in an effort to break it open. When thirsty, they may hammer out a crude watering hole into the ground using a rock. These general patterns, as well as some of the clade-specific specialisations, probably have a long history among New World monkeys (Rosenberger, 1992) but the current situation is also an imperfect guide to how the ecology was structured in the past. The Amazonian seed-eating monkeys, sakis (*Pithecia* and *Chiropotes*) and uakaris (*Cacajao*), for example, have fossil relatives equipped with a very similar morphology that lived far to the south, in Patagonia, approximately 17 Ma. Although their reliance on heavily protected, woody-shelled fruits seems rare in the context of the modern radiation, and their current count of only three extant genera also might suggest these animals are an odd offshoot of the radiation, this

group was actually quite diversified in the past and may at times have been a dominant taxonomic assemblage (Rosenberger, 2002).

New World monkey social groups range in size from individual pairings of titi and owl monkeys to large and gregarious groups in the woolly monkeys, squirrel and capuchin monkeys and the sakis and uakaris. The latter groups represent three distinct lineages where relative brain sizes have also become enlarged, independently, probably as a correlate to evolving large, complex social groups (Hartwig *et al.*, 2011). In contrast, the pair bonded titi and owl monkeys have relatively small brains. Mating strategies also vary among the platyrrhines and parallel several catarrhines in structure. For example, the owl and titi monkeys are monogamous, much like gibbons (some callitrichine are also polyandrous); spider monkeys and muriquis are polygamous and organised as fission–fusion social groups, resembling chimpanzees; howler monkeys may be organised as one-male harems, like gorillas. But in contrast to most Old World monkeys and apes, only a few platyrrhines display high degrees of sexual dimorphism as a result of intense male–male competition for mates, and body size is not generally linked to its expression. Muriqui are the largest living platyrrhines and among the least dimorphic, in spite of behavioural similarities shared with chimps, who are dimorphic. As an alternative to physical contests, male muriki employ sperm competition. At the other end, the lightweight, lithe squirrel monkeys are an interesting example where sexual dimorphism is strongly and permanently expressed in the canine teeth, much less so in body mass. But their unique social situation brings with it unusual periodic measures. They live in large, sexually segregated groups and males also undergo a mating season change in size and appearance to masquerade as tough guys. They temporarily gain size and weight, visibly concentrated in the shoulders, as each one bluffs and occasionally fights his way towards mating success. **See also:** [Sexual Selection](#)

Callitrichine New World monkeys are the only anthropoid primates that routinely give birth to fraternal, non-identical twins, sometimes twice a year if food is plentiful. Except for one species, the callimico, which produces singletons, callitrichines display the most prodigious reproductive potential of any anthropoid primate. The callitrichine reproductive system is highly unusual in other respects as well. Some species are known to have chimeric offspring, meaning the twins exchange stem cells *in utero*, making it possible that an embryo may inherit the genes of an uncle that were passed to the mother one generation prior, during the gestation period she shared with her own twin brother (Digby *et al.*, 2011). Another interesting life history characteristic has been documented in squirrel and capuchin monkeys, where growth rates have been studied. These cebines have among the largest relative brain sizes among New World monkeys, but they arrive at this state through opposite prenatal and postnatal patterns. The squirrel monkey has an extended gestation length for its body size and gives birth to an extremely precocial

newborn. By contrast, at least half of the neural growth in capuchins takes place after birth, after a gestation of normal length. **See also:** [Reproduction in Eutherian Mammals](#)

## Fossil History

The fossil record of New World monkeys samples their adaptive radiation in only the barest detail. At the present time more than two dozen extinct genera are recognised (**Table 2**), but they span almost 27 million years (My) of time and have been found in only five different geographic areas. These include discoveries in Bolivia, where the oldest platyrrhines, *Branisella* and *Szalatus*, have been discovered, and in Argentina, Chile, Colombia, Brazil and the Caribbean islands. Most of the fossils are concentrated in Colombia. Because four of these five regions are geographically peripheral to where most New World monkeys live today, it seems evident that the past biodiversity of platyrrhines almost certainly exceeded that of the living forms.

None of these discoveries have thus far shed light on platyrrhine origins, which is an exciting and much debated question: Did the first New World monkeys arrive from North America or from Africa? This fascinating puzzle has been discussed since before Darwin's time, but it remains without a satisfactory explanation because any passage from the two most likely continental sources for the ancestors of platyrrhines would most likely have required an open water crossing of some considerable distance at approximately 35–40 Ma, which is when they are thought to have arrived. Clues that the platyrrhine stock originated in Africa have gained more support in recent years as it has been shown that a large taxonomic group of rodents that are also uniquely South American, the relatives of guinea pigs (caviomorphs), may also have an African ancestry, although they probably got there earlier than the monkeys. Unfortunately, palaeo-oceanographers have not been able to identify island landmasses of a convenient size and place situated in the Atlantic Ocean that would have shortened their voyages by providing a liveable archipelago, stepping stones or temporary land bridges. And, it is hard to imagine a breeding group of monkeys surviving more than a few short days stranded aboard a mass of vegetation baking in the sun while floating on the high saltwater seas. Other, less trenchant palaeontological clues serve as reminders that interchange between eastern Asia and North America was occurring among early primates, and several orders of mammals got to South America from North America during earlier times. So, at this point, the objective evidence may lean a bit toward an African source, but the route preplatyrrhines might have taken in winding their way to South America is a matter of speculation, as is their final staging area. The climate was known to be favourable, and primate dispersal routes among the northern continents were open 15–20 My prior to the platyrrhine's arrival, when it took approximately 25 000 years for the early primate *Teilhardina* to get from central China to western



**Figure 5** Five views of a fossil platyrrhine cranium, *Antillothrix*, found in an underwater cave in the Dominican Republic. The palaeontology of such caves is currently the major source of fossil mammals and other vertebrates from the Dominican Republic. © Alfred Rosenberger.

North America via Europe and across the North Atlantic (Smith *et al.*, 2006). **See also:** [Adaptive Radiation](#); [Fossil Record](#)

One remarkable aspect of the New World monkey fossil record is the frequency with which extinct taxa bear close resemblance to living species. Fossils as far back as the early Miocene share anatomical traits with living New World monkeys, at the taxonomic levels of subfamily and tribe. The fossil-rich middle Miocene site of La Venta in Colombia has yielded at least four genera that are quite closely related to modern forms and some, like those related to owl and squirrel monkeys, are reasonable direct ancestors to living species. At that time, the now arid intermountain La Venta region was an extension of the Amazon basin, which was being transformed into its modern self. Equally interesting are two nearly complete skeletons (Cartelle and Hartwig, 1996; Hartwig and Cartelle, 1996) recently recovered from Brazilian caves dating to the Pleistocene period, which have demonstrated that some platyrrhines (*Caipora* and *Protopithecus*) were once twice as large in body size as the largest living species (Halenar, 2011). The three Greater Antillean islands of the Caribbean are also producing fossils (Figure 5), most spectacularly from underwater caves in the Dominican Republic where they are being recovered by scientifically trained scuba divers (Cooke *et al.*, 2011; Rosenberger *et al.*, 2011a). Although they might be only a few thousand years old, like the extinct ground sloths that also got marooned on these mammal-poor islands, the fossil monkeys tend to resemble archaic species including several known from the early Miocene of Argentina, attesting to the early isolation of a stock that may have splintered off before the modern

adaptive radiation evolved its place in the Amazonian ecosystem. **See also:** [Phylogeny and Stratigraphy Comparison](#)

## Phylogeny

In the past few decades, the results of morphologists and molecular biologists have begun to converge in the effort to build a tree and timescale of platyrrhine evolution. Some long-suspected close relationships have been supported through numerous studies of both anatomy and genetics, whereas some long-debated relationships continue to be ambiguous irrespective of approach. In general, the monophyletic affinities of genera now classified as Atelidae, Pitheciidae and Callitrichinae are supported strongly by molecular and morphological studies. The unity of the Cebinae, which had not been widely recognised, and their close affinity with callitrichines, which was only first proposed in the late 1970s, is firmly supported also. The most recent molecular studies (Perez *et al.*, 2012), however, fail to ‘confirm’ a clear picture of the evolutionary position of *Aotus*, a genus long thought to be linked with *Callicebus* on morphological grounds, whereas both approaches confirm that titi monkeys are closely related to sakis and uakaris, a point that also was first demonstrated anatomically in the late 1970s. Another facet that has become mutually corroborated by fossils and morphology is the antiquity of these several lineages. All are represented by fossils 11–13 My old at La Venta, Colombia and some go back much further in Patagonian Argentina, where 17–20 My old representatives of modern clades existed (Rosenberger *et al.*, 2009; Rosenberger, 2011), and perhaps even



sister-group relatives or ancestors of modern genera, like the owl monkey. **See also:** [Molecular Phylogeny Reconstruction](#)

This picture of longevity for the existing radiation contrasts with the catarrhines, where lineages more than 10 Mys old are rare and the longest persisting modern genus is considerably younger (Delson and Rosenberger, 1984). Why the evolutionary pattern differs so profoundly among platyrrhines may be due partly to palaeogeography. Although both New and Old World tropical habitats contracted in the Miocene as the world's grasslands flourished, the South American continent remained isolated physically, except for a trickle of North American non-primate mammals able to cross in the region of Panama during mountain building episodes beginning approximately 10 Ma. Locked within the continent, platyrrhines differentiated early into their manifold arboreal adaptive zones and they were not overtaken, either by any outsiders in need of the same resources or by a foreign splinter lineage that may have been established elsewhere on the continent and later grew to extirpate the entrenched radiation. To the contrary, it seems likely that several southern platyrrhine fossils are simply older versions of the northern ones. Across the Atlantic, however, there were several periods where the continental plates of Africa, Europe and Asia shifted positions and boundaries, and sea level falls permitted habitats and fauna to mix. This may have allowed a turnover of primates. The earliest African forms that were essentially primitive anthropoids, for example, were replaced by primates related to apes, who in turn were out-competed by the monkeys. Although we do not know where the Old World monkeys first arose, they were probably terrestrially adapted at first and later moved back into the trees to out-compete the smaller-bodied arboreal apes. So, the potential for lineage extinction was probably more prevalent among Old World anthropoids than the New World forms.

The phylogeny of New World monkeys is also a lesson in the interconnectedness of genealogy and adaptation, in ecophylogenetics, as an evolutionary process as well as an approach to studying them. In the broad sweep of their evolutionary history, the key driving force in the adaptive radiation of the living New World monkey clades (and genera) has been the diverse exploitation of key feeding niches. What most distinguishes the subfamily groups from one another is their alternative and complimentary adaptations to foraging styles and feeding niches, and the characteristics used to recognise both phylogeny and adaptations are often the same. The focus of atelines on upper canopy leaves and fruits, for example, starkly contrasts with the inclination of callitrichines to use the lower canopy tree gums, botanica and invertebrate fauna; derived specialisations of the masticatory apparatus and locomotor system lead to that interpretation. To the extent that the evolution of feeding niches is the story of New World monkey phylogeny, a basic bifurcation between frugivore–faunivores on the one hand (Cebinae and Callitrichinae) and frugivore–folivores (Atelidae and

Pitheciidae) on the other may represent the adaptive essence of the earliest phylogenetic splits among the living forms (Rosenberger *et al.*, 2009).

However powerful this analytical approach is, and how accurately it may reveal history, this ecophylogenetic hypothesis may account only for the modern radiation of New World monkeys. What came before remains an open question. Although the fossils go back as far as 27 Mys, the molecular trace embedded in the living species' genomes converges to an ancestry that may reach back 35–40 Ma or more (Poux *et al.*, 2006). To comprehend what those monkeys looked like, what they did to make a living ecologically and where they came from in the first place, will require much more fossil evidence than what is currently in hand. **See also:** [Adaptation and Natural Selection: Overview](#)

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