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CHAPTER 1

# WHAT IS A NEW WORLD MONKEY?

This book is about the evolutionary odyssey of New World monkeys, the South and Middle American platyrrhines, though it is mostly about their evolution in South America where most of platyrrhine history was played out. Their odyssey appears to have begun 45–50 million years ago when an ancestral population of monkeys arrived in South America to found one of the most diverse and colorful adaptive radiations produced by the Order Primates. A robust view of what platyrrhines have become and how can be gleaned from the living animals today and the fossil record, which, though still limited, documents the major features of New World monkey evolution during roughly the last 25 to 35 or 40 million years of their existence, although the record is exceedingly sparse for periods older than 20 million years. Unlike other major primate groups, the history of New World monkeys is one in which the separate lines of descent leading to many of the 16 extant genera recognized herein can be traced back in time for millions of years by fossils and by molecules. This long-lineage pattern is what gives the structure of platyrrhine evolution its distinctive shape, and it is a centerpiece of this book. It also serves as a poignant point of reflection in thinking about the platyrrhines' future. Fourteen of the 16 living genera include species that are now classified, according to the International Union for Conservation of Nature (IUCN), as Critically Endangered or Vulnerable.

There is an abundant record of fossil South American mammals that dates back nearly to the beginning of the Age of Mammals, about 66 million years ago. However, the oldest New World monkeys we know of date back only 36–40 million years. Given that South America was an island continent for most of the last 66 million years, as the world's living mammals began to flourish and before Isthmus of Panama emerged to firmly connect North and South America 3 million years ago, the questions arise: Where did their ancestors come from, and how did they get there? Whether primates originally came from Africa by rafting across the Atlantic Ocean on a floating mat of vegetation, or mostly overland from North America, two scenarios detailed in

chapter 10, they arrived as pioneers in a landscape where monkeys had never existed before.

The ways in which these animals evolved and thrived on the isolated continent, always in the trees, is a history of radical change and enduring stasis, novel adaptive solutions and predictable transformations. It is a story of giants, dwarfs, brainy predaceous tool users, dim vegetarians, fungus feeders, and bark-gnawing gum eaters. It is an account of cautious quadrupeds, acrobatic arm-and-tail swingers, quiet nocturnal denizens, and roaring diurnal howlers. Their mating strategies include codominant monogamists, and alpha males and alpha females living in large social groups. In some species females use scent to control the breeding success of their daughters; in another, males queue up on big branches waiting their turn to copulate with one female. By inhabiting a range of niches so varied in ecological and anatomical solutions to feeding and locomotion, or in social arrangements for group living, mating, and rearing offspring, platyrrhines have produced one of the most diverse adaptive radiations among the primates.

How did this happen? The present is key to understanding the past. There are two intertwined models describing how platyrrhine evolution has unfolded, the Long-Lineage Hypothesis and the Ecophylogenetic Hypothesis. What this means is that the many kinds of monkeys we see today have been around for millions of years and that some have existed for at least 20 million years with little change in their ecological situation, to the extent that their adaptations are documented in the fossil record. Furthermore, at another level, genetically related subgroups of New World monkeys, clusters of genera linked by their shared phylogenetic histories, have found success in various ecological niches defined by the particular sets of characteristics inherited from their remote common ancestors. Today, more than a dozen extant platyrrhine species belonging to all the six major subgroups can be found packed into a single rainforest locality, forming a harmonious monkey community. The fossil record suggests that this phylogenetic and ecological framework may have been in place for the entirety of the modern platyrrhines' long-lived existence, setting the stage for the evolution of more refined divisions of niches by the procession of the living genera and species.

As further discussed below, I use the term lineage to mean a genus-level line of descent, an evolutionary stream carried in DNA that is embodied in a species, or a collection of intimately related species, and is manifested as a distinct ecological lifestyle. When examining an entire radiation such as the platyrrhines, the taxonomic level of genus, not species, is the most appropriate perspective. Genera exemplify and define the combinations of anatomical
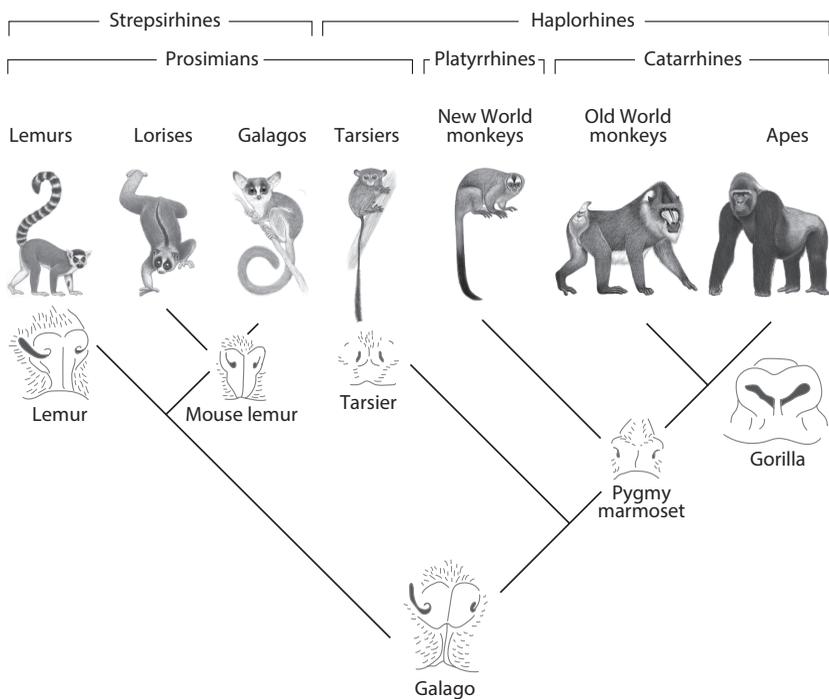
**FIG. 1.1.** Cladogram of the major groups of living primates mapped with the distribution of external nose shapes. Primate images courtesy of Stephen Nash.

and behavioral characteristics that are of particular ecological relevance, and that separate all the significant lines of descent that compose an adaptive array.

## What is a monkey?

We regularly call platyrrhines monkeys, but the word monkey has no scientific significance. There are two groups of primates commonly called monkeys, the New World monkeys and the Old World monkeys. However, they are not grouped together in formal taxonomic language because they lack the evolutionary connection that is the main reason animals are classified jointly in particular groups: a genetic, or phylogenetic, relationship. The two groups we call monkeys are less closely related than the use of the word monkey suggests. In fact, the primates we call Old World monkeys, such as olive baboons and the rhesus macaques, are more closely related to apes than they are to New World monkeys (fig. 1.1). New World monkeys are a separate group

entirely, an offshoot of the primate family tree that appeared about 25 million years before the earliest appearance of today's Old World monkeys and apes documented in the fossil record. The sameness implied by the word monkey is an anachronism that may date back to the 14th century, according to the Oxford English Dictionary, an old-fashioned word based on an equally old, pre-evolutionary idea about the natural world. It was meant to distinguish these animals from apes and the other nonhuman primates, the lemurs, lorises, galagos, and tarsiers of Africa and Asia. They are all very different from monkeys and apes in many ways, including the structure of their skulls, their dentition and skeletons, sensory systems, and behavior, reflecting separate evolutionary histories.

Taxonomic groups that are formally recognized and named as units in classifications, such as species, genus, family, and order, are called taxa, the plural form of the word taxon. The term taxonomy, which means arrangement, is derived from the words taxon and taxa. The groups mentioned thus far—primates, platyrrhines and New World monkeys, Old World monkeys, apes, tarsiers, lemurs, lorises and galagos—are all taxa that have formal names in classifications as well as these common names. But monkey is not a taxon and has not been thought of in that way since Darwin introduced us to evolution and phylogeny, and reinforced the notion that classification should be based on relatedness, which previously was only a vague idea. The word is applied to two different groups of taxa that are actually not each other's closest relatives.

Some labels for primate groups are like nicknames and have no scientific standing. Sometimes they are holdovers from the pre-Darwinian period when natural history was not a secular enterprise and scholars used such terms to express their ideas about how far a group was stationed along an imagined trajectory, a ladder of ascent, reflecting the Scale of Nature or the Great Chain of Being that emanated from Creation. Humans were considered the pinnacle of creation and all other animals were said to occupy standings below that high point, as lower grades or stages in the procession of life. The early naturalists arranged their classifications accordingly and their informal language sometimes expressed those views. Thus the term monkey referred to the group of primates grouped with the apes as "higher primates" and gradistically situated between apes and the "lower primates," the tarsiers, lemurs, lorises, and galagos. The latter were called prosimians, meaning near monkeys and apes. Eventually, Darwin made it quite clear that the two great groups of monkeys were distinct: Old World monkeys are the closest living relatives of apes and New World monkeys are a separate line of evolution within the monophyletic group—the unique descendants of a

common ancestor—we call Anthropoidea, informally anthropoids, the taxonomic equivalent of "higher primates," composed of New World monkeys, Old World monkeys, apes, and humans.

Even in the Darwinian era grade-thinking persevered throughout biology, and particularly when it came to discussing nonhuman primates as human relatives. Darwin's most effective scientific ally, Thomas Henry Huxley, wrote of primate diversity and evolution in 1863, in *Man's Place in Nature*, four years after *On the Origin of Species* was published. He said, "Perhaps no order of mammals presents us with so extraordinary a series of gradations as this—leading us insensibly from the crown and summit of the animal creation down to creatures, from which there is but a step, as it seems, to the lowest, smallest, and least intelligent of the placental Mammalia." In the next 100 years the gradistic mindset faded from research practice but it still endures in our everyday language as a convenience, hence the word monkey. As a way of viewing the world, however, gradistics failed with the onset of a methodological revolution known as cladistics that occurred in the 1960s, which sought to organize and classify groups according to their placement on the appropriate branch, or clade, of the phylogenetic Tree of Life, as will be fully discussed later. That failure had important consequences in spurring a wholesale re-thinking of platyrrhine evolution.

The geographic modifier in the name New World monkey is also an anachronism. Since the Age of Discovery, in the 15th century, European writers have referred to the Western Hemisphere as the New World, ostensibly discovered by Columbus, in contrast to the Old World, comprising Eurasia and Africa. Similarly, platyrrhines are also often called Neotropical primates, meaning primates of the New World tropics. In an ecological sense, that term may conjure up a misunderstanding about the habitats where platyrrhines live, and what the relevant environments of South America in particular look like. It delimits the wide swath of South and Central America straddling the equator, the tropical zone, where the climate is moist, warm or hot all year round and supports dense, evergreen, jungle vegetation. But that landscape is not all continuous rainforest, and platyrrhines are not strictly jungle dwellers.

South America is a vast continent that is two-and-a-half times the size of the Amazonian rainforest, where most platyrrhines are found. Another vitally important tropical and subtropical region, the Atlantic Forest of southeastern Brazil, supports a smaller, unique ensemble of monkeys including several endemic forms, meaning they are found nowhere else in the world (fig. 1.2). Most of them are presently endangered as a result of the wholesale decimation of the Atlantic Forest that occurred during the last 500 years which, as discussed in chapter 11, has reduced their habitat to disconnected, relict forest fragments
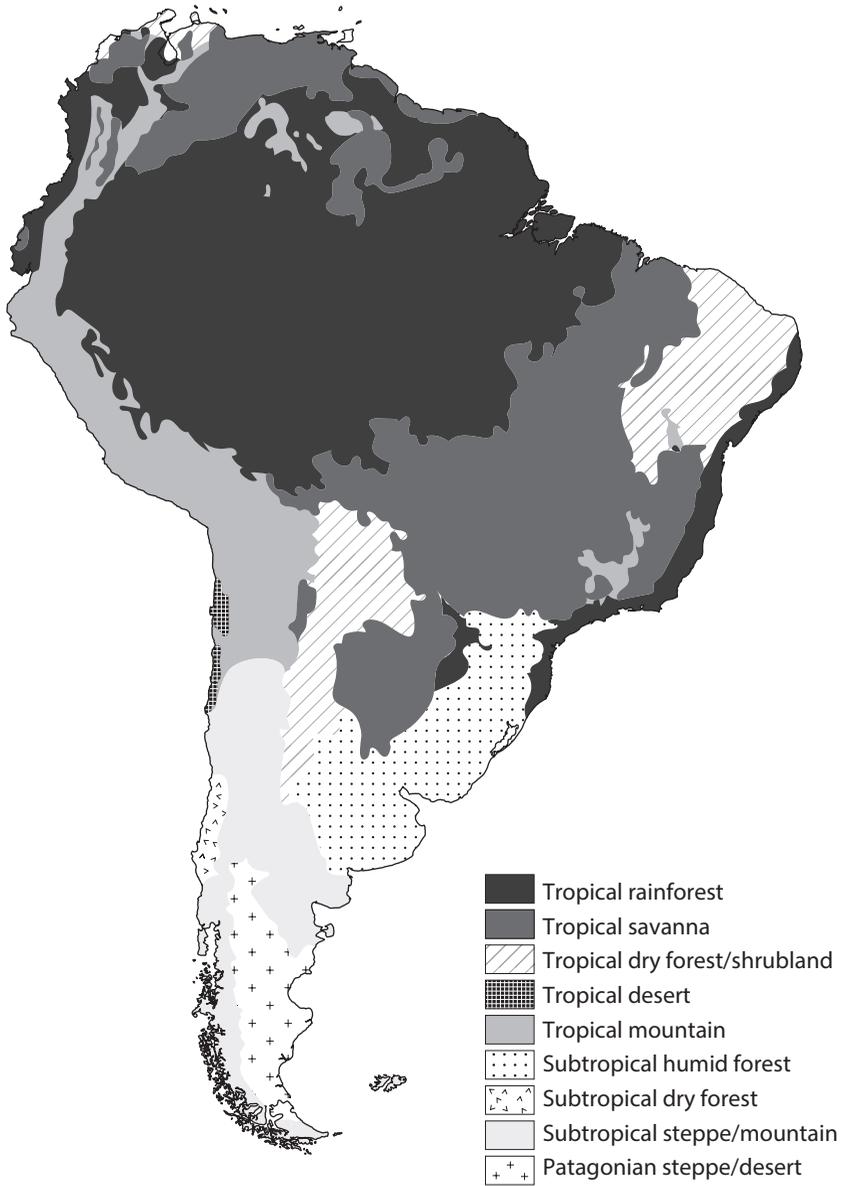
**FIG. 1.2.** Map of South America and its major ecological zones.

Tropical rainforest
Tropical savanna
Tropical dry forest/shrubland
Tropical desert
Tropical mountain
Subtropical humid forest
Subtropical dry forest
Subtropical steppe/mountain
Patagonian steppe/desert

about one-tenth the size it was when European colonists first arrived in Brazil half a millennium ago.

The full geographic range encompassed by monkeys in South America extends from the northern edge rimming the Caribbean Sea and the Atlantic and Pacific Oceans, to northern Argentina in the distant south. The habitats mapped out in this enormous expanse are predominantly evergreen rainforests, semideciduous forests where trees lose their leaves seasonally, and open-country savannas, grasslands, and shrublands. Primates can be found in all these areas, though the greatest concentration of species and the most densely packed communities of platyrrhine species occur in the rainforests. In drier, more sparsely vegetated zones, only a few generalist species of monkeys, or those with a special set of adaptations to procure food from a limited, local supply, manage to get by. There they are often found in narrow strips of forest situated alongside water courses. Of all things, New World monkeys need trees no matter where they live.

Why is this so? Comparing the vegetation map of South America with the distribution maps of the living species highlights an intensely interesting question about platyrrhine evolution: Why are there no terrestrial species? In Africa, another enormous continent with a similarly varied distribution of habitats, Old World monkeys have evolved an impressive array of terrestrial and arboterrestrial species, living in forests and even extending into bone-dry, near-desert areas. In contrast, while platyrrhines are obviously an exclusively arboreal radiation, there is nothing about the design of their bodies or their dietary needs that makes it impossible for a New World monkey to habitually visit the ground and benefit from it. Actually, some species do so occasionally in order to cross large gaps in the forest or obtain drinking water in drier places when the forest does not provide them with enough because watery fruits are in short supply.

Juvenile monkeys sometimes play on the ground. Clever capuchin monkeys living in swampy areas have even learned to collect clams on the ground when the tide recedes. Yet, no living platyrrhines have evolved terrestrial adaptations or a terrestrial lifestyle. Given their long evolutionary history, however, and knowing that South American forests have waxed and waned over the entire continent, it may be that the fossil record will at some point turn up a ground-dwelling New World monkey. In fact, there is already a hint of this in the few remains of an extinct Caribbean platyrrhine, *Paralouatta*, to be discussed in a later chapter. With all that biologically built-in ecological flexibility and a vast area of the continent as potentially exploitable habitat, under the forest canopy and beyond, the absence of living terrestrial platyrrhines seems quite the mystery.

### What is a platyrrhine?

The technical name for New World monkeys is Platyrrhini; platyrrhines, colloquially. It means flat- or wide-nosed. The name was given to them in 1812 by the French naturalist Étienne Geoffroy Saint-Hilaire, who was then sorting and cataloging specimens of mammals held in the collections of the Muséum National d'Histoire Naturelle in Paris. He found that the shape of the nose turned out to be a useful way to identify several groups of primates. In platyrrhines the nostrils are widely spaced and laterally facing, separated by a broad fleshy strip between the openings (fig. 1.1). In some, such as the Saki Monkey, the expression of this characteristic is rather extreme. A contrasting pattern occurs among Old World monkeys and apes, which have nostrils that are closely spaced and separated by a thin band of flesh. They are classified as Catarrhini; catarrhines, informally, meaning downwardly facing nose.

These distinctions, like many others used in identifying and classifying primates, are exhibited consistently among platyrrhines, but not universally. To see an exception, one has only to look at the gorilla-like face and nose of the largest living platyrrhine, the Muriqui, with its adjacent nostrils. The usefulness of employing these names, terms stemming from the same Greek root word for nose, *rhine*, is that they are physically descriptive and they bind together a naturally paired, phylogenetic set of primates. Platyrrhines and catarrhines are the two branches of the extant anthropoid primates, the taxonomic group consisting of New and Old World monkeys, apes, and humans that arose monophyletically from an exclusive common ancestor.

Because the nose is made of flesh, which under nearly all circumstances does not fossilize, paleontology is limited in what it can tell us about the evolution of the platyrrhine nose, and the contrasting catarrhine pattern as well; but is there is a way to reconstruct their morphological histories by examining the living animals? If so, what would the nose have looked like in the last common ancestor of anthropoids? Would its shape have been platyrrhine, catarrhine, or something else? In other words, what nose shape is the primitive form in anthropoids?

In fact, we have good reason to infer that in the first anthropoids the nose was platyrrhine-like. To arrive at that interpretation, we use information on the comparative soft anatomy of extant animals in order to envision the past, as a hypothesis, with an assist from fossil evidence. This method, called character analysis, involves examining the similarities and differences of inherited traits—or presumably inherited, since links between genes and anatomy are still difficult to establish—in closely related forms, with the aim of tracing the sequence in which the details of those features evolved. The approach applies

to any observable trait and it is important for understanding how and why evolutionary changes happened functionally, although it does not always lead to adaptive insight because we often do not know the benefit of one pattern or another even when they are linked historically.

In the case of noses, character analysis entails invoking the primate clado-gram, a simplified family tree, as a map that guides us toward the common morphological denominators shared between the animals in question and their nearest relatives: platyrrhine and catarrhine noses are compared with the nose of the tarsiers of Southeast Asia (fig. 1.1). Tarsiers are small, giant-eyed, noctur-nal predators, and they have an external nose that is a close match for a platyr-rhine's even though most of the animal's other features look almost nothing like a platyrrhine or any anthropoid. Since its broad, laterally facing nostrils and pug nose conform to the New World monkey pattern, we can infer that the ancestral anthropoids also shared that morphology, perhaps comparable to a pygmy marmoset's.

The scientific logic behind this conclusion is that it is the most parsimo-nious, or efficient, explanation of the taxonomic distribution of nose shape among the three groups. Reasoning this way implies that New World monkeys inherited a tarsier-like pattern with little change from the original condition, and that catarrhines later evolved the newer, derived shape. An alternative inference would hypothesize that the catarrhine shape was ancestral in an-thropoids. But that means we would have to explain why the same wide-nosed morphology evolved twice in this one monophyletic group, once in the line leading to tarsiers and a second time in the ancestors of New World monkeys. Minimizing such parallelisms, which means minimizing the number of hy-pothesized evolutionary changes required to satisfy existing morphological and taxonomic conditions when there is no reason to think otherwise, is basic to the protocol of the character analysis strategy. That's what is meant by par-simony, and explanatory efficiency. Regarding the evolution of the two nasal shape patterns in this exercise, we still have no sound explanations concerning functional significance, but we do have possible explanations for some of the more oddly shaped, superwide external noses found in a few living platyr-rhines, such as the Saki Monkey, as we shall see below.

Focusing on the nose to identify a primate or other mammal, and formal-izing it descriptively in the structure of a taxonomic name, is a common prac-tice in mammalogy. The rhinoceros, formally the genus *Rhinoceros*, meaning horn-nosed in Greek, is a familiar example. Among catarrhine primates, there is the Proboscis Monkey, *Nasalis*, meaning of or pertaining to the nose in Latin, a genus in which females have a striking, projecting nose and males have an extremely large, pendulous nose.

It may seem odd or even trivial that scientists continue to sort major, higher taxonomic groups of primates such as the platyrrhines and catarrhines by the shapes of their noses because of a tradition dating back to the early 1800s, particularly if we have few ideas about any adaptive significance or benefit to the different morphologies. True, nose shape once served as nothing more than a convenient descriptor and identifier for early naturalists who had limited knowledge of the deeper anatomy, or the actual lives, of the animals whose remains they studied. But as understanding of anatomy and behavior accumulated, this approach began to yield important clues about primate evolution.

The Order Primates is divided into two major extant groups (fig. 1.1), called Strepsirhini (strepsirhines) and Haplorhini (haplorhines). The extant strepsirhines include lemurs, lorises, and galagos. They have wet noses with slitlike, comma-shaped nostrils: strepsirhine, from the Greek *streph*, means twisted nose, a reference to the shape of the nostril's opening. The haplorhines are tarsiers, New World monkeys, and Old World monkeys, apes, and humans. They have dry noses with rounded nostrils. *Hapl*, also Greek, means simple, an illusion to the rounded nares.

We now understand that these names represent profoundly different biological systems. They are only parts of a larger anatomical complex that is functionally and behaviorally important in regulating communication and even how these animals tend to perceive the world, how the two groups gather fundamental information about their surroundings. While all primates are highly competent visual animals, the strepsirhine primates, which are mostly nocturnal and live in low-light conditions, favor olfaction over vision as sensory input. Their acute sense of smell is tied to the structure of their noses. Haplorhine primates, who are mostly diurnal, favor visual input over olfactory information. Consequently, they are less dependent on the anatomy of the nose, and the snout has evolved in another direction.

The outward, easily seen differences in nostril shape, traits that are still without a good adaptive interpretation, are accompanied by other, functionally significant features. A slit or rounded nostril is one piece of a more important whole, the nose itself. Strepsirhines have a bulbous external nose, much like a dog's, covered in a perpetually moist, textured skin. Situated at the very tip of the bony snout, the nose extends as a broad flap directly into the mouth, and splits the hairless upper lip in the middle. As a result, the mouth is not ringed by muscle, and no lemur, loris, or galago is able to control the contour of their lips to shape the mouth to produce facial expressions—no smiling, grimacing, or pouting.

The textured surface of the wet nose is designed to collect molecules of scent from the air they breathe and shunt them down a strip of skin toward

a chemosensory organ, the vomeronasal, or Jacobson's organ, situated in the mouth behind the upper incisors. It is part of the secondary olfactory system that is the seat of pheromonal communication, a scent-based adaptation that is especially important in the exchange of sexual signals between males and females. The primary olfactory system, which has sensors located in the nose itself, is concerned with the broad range of environmental smells. The processing centers of the strepsirhine brain, of course, are coordinated, and they emphasize the olfactory areas rather than the visual ones. As one example of this pattern, the forebrain has a conspicuously large olfactory bulb in strepsirhines, while the area responsible for processing visual information in the back of the cerebrum, the occipital lobe, is not emphasized.

Haplorhines have dry, non-textured, untethered external noses, separated from the mouth by a continuous, fleshy, mobile upper lip and a patch of furry skin. A secondary olfactory system still exists in some haplorhines, but it is greatly reduced. Bands of muscle encircling the mouth are buried in the upper and lower lips of haplorhines, giving them varying levels of freedom to shape the mouth in communication. The occipital lobe important to visual processing is well developed, while the olfactory lobe is reduced compared with strepsirhines. With a haplorhine-based potential for elaborating the mobility and importance of the lips, among platyrrhines the capuchin monkeys have evolved well-differentiated oral musculature, which makes it possible for this monkey to produce grins, grimaces, smiles, frowns, puckers, and a host of other visual gestures and sounds to support its sophisticated forms of communication.

There are other important structural features of the cranium, and the eyes, that relate to the differences between the strepsirhine and haplorhine primates, and the trade-offs each of these groups has evolved in supporting what we generally think of as a smell-dependent or sight-dependent lifestyle. For example, the eyes of strepsirhines, which are designed for night vision, are set wide apart. They are separated by the structure of the cranium, by the space where the large olfactory bulb is situated, and by the rear end of the capacious chamber that makes up the bony nose inside the rostrum, which houses an impressive array of scroll-like bones covered in smell-sensitive epithelial tissue. The eyes of haplorhines are set closer together. They are designed for daylight, and the hollow that forms the bony nose is much smaller in volume, with a much smaller complement of olfactory scrolls.

As far as spelling goes, if there appears to be an inconsistency in forming these *rhine*-based, compound, informal taxonomic names—strepsirhine, haplorhine, platyrrhine, and catarrhine—it's not a typo. In spite of a recent push for uniformity, to employ the comparable double-*rr*, platyrrhine-catarrhine

spelling when writing the strepsirhine and haplorhine terms, it was decided in this volume to maintain these single-*r* spellings because it adheres to common, published usage established over more than a century, thus preserving continuity of language. Doing so does not conflict with the ethos of taxonomy or zoological nomenclature. There are no naming rules for categories above what we refer to as the family level, meaning terms given to formal taxonomic classes like Superfamily, Family, and Subfamily. At the same time, a major tenet of the rules of nomenclature to which zoologists abide stresses the conservation of names to maintain clarity.

## Platyrrhines and catarrhines

As the field of comparative anatomy grew in the 1800s, a variety of cranial and dental features were discovered to distinguish extant platyrrhines and catarrhines in addition to their nasal morphologies (fig. 1.3). For example, the sidewall of the cranium in the region where the braincase joins the face on the backside of the orbit is composed of several bones that fit together like puzzle pieces to form what is called the postorbital mosaic. In platyrrhines, the mosaic is completed horizontally by a suturing of the zygomatic and parietal bones. The postorbital mosaic of catarrhines is closed vertically, by a suturing of the frontal and sphenoid bones. As with the platyrrhine vs. catarrhine external noses, the differences are consistent yet there are exceptions. What these contrasting suture patterns mean functionally, if anything, has not yet been determined.

A third trait distinguishes New World monkeys from Old Word monkeys and apes. It is the shape of the ectotympanic bone that supports the eardrum, or tympanic membrane, by encircling it (fig. 1.3). The vibration of the eardrum initiates hearing when it is struck by sound waves traveling through the air. In platyrrhines, this thin bone is an open, ringlike or U-shaped loop that sits flatly against another bone that houses the hearing mechanism, thus producing a prominent "hole" in the ear region. In catarrhines, the ectotympanic bone is shaped like a tube, more or less horizontally disposed. Its medial (inner) end holds the tympanic membrane in place and its lateral (outer) end opens to the auditory environment. Because the tubular ectotympanic bone narrows laterally, catarrhines tend to have a relatively smaller opening that can be seen on the side of the cranium.

A fourth trait that distinguishes platyrrhines from catarrhines is the dental formula, or tooth count (fig. 1.3). By convention, the dental formula enumerates the teeth in each functional tooth group—incisors, canines, premolars, and molars—in the four quadrants of the mouth—right, left, upper, and lower.
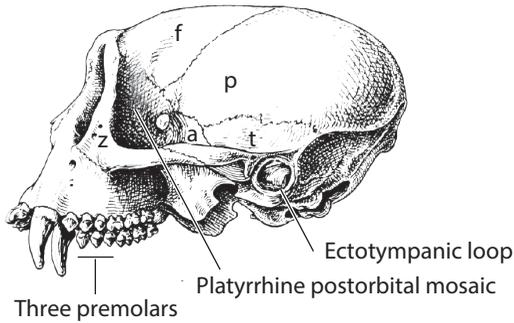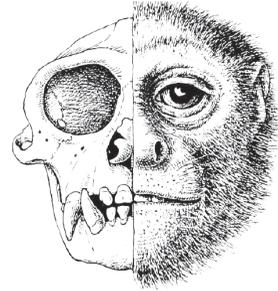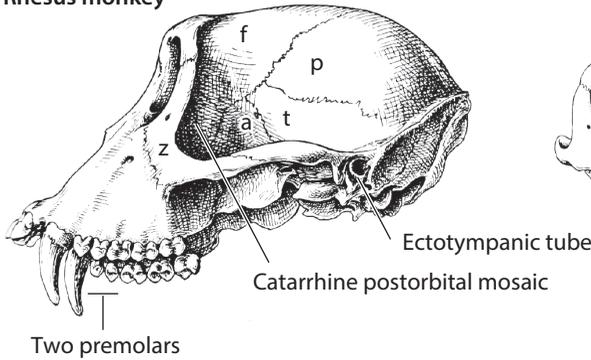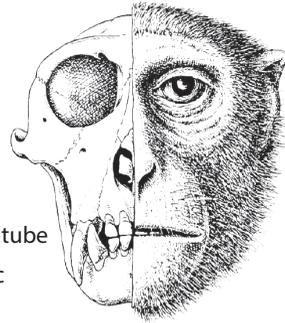
**FIG. 1.3.** Skull and face of a capuchin and a rhesus monkey showing cranial features that distinguish modern platyrrhines and catarrhines. Abbreviations of bone names: a, alisphenoid; f, frontal; p, parietal; t, temporal; z, zygomatic. Adapted from Schultz (1969).

When the count is the same in the upper and lower jaws, the pattern can be described using a simple string of numbers. Living platyrrhines have two dental formulae because the numbers of molars differ among genera, but they always have three premolars. Their dental formulae are: 2-1-3-3 and 2-1-3-2. Among the extinct platyrrhines, an unusual genus from the Caribbean also has a reduced count of two molars. The contrasting formula among living catarrhines is 2-1-2-3. One premolar has been lost. This shortens the non-molar, front end of the toothrow, a shift that indicates an emphasis on chewing food with the molars, whereas New World monkeys have maintained an emphasis on the premolar battery for biting, a processing step that precedes molar-mastication.

The hard-anatomy differences between platyrrhines and catarrhines, which had been diagnostic for more than a century, came to be revised in the mid-1960s when Elwyn Simons, the great American primate paleontologist, discovered the fossil *Aegyptopithecus zeuxis* and other 30-million-year-old anthropoids in the Fayum Depression, a geological basin south of Cairo, Egypt. The Fayum has produced an extraordinary trove of material that exponentially increased the fossil record of early Old World primates and other mammals of this period. It led to the discovery that the archaic Old World anthropoids of that age resembled living platyrrhine morphology rather than the extant catarrhines in two of the four diagnostic features, in having a three-premolar dental formula and a non-tubular ectotympanic bone. As far as the other two distinguishing features discussed above, the earliest Egyptian fossil crania are ambiguous as to the morphology of the postorbital mosaic, and, of course, none of them inform us about nasal shape.

There is, however, an opportunity to discover more about the olfactory behavior of Fayum primates by examining the bony anatomy inside the nasal opening. It can provide clues about the secondary olfactory system that, as mentioned, is well developed in strepsirhines and plays a role in communication via scent, especially in connection with reproduction. The nerve that joins Jacobson's organ to the brain runs in a midline groove that is observable in some well-preserved fossil crania. The width of the groove corresponds to the thickness of the nerve. A study of *Aegyptopithecus* crania reveals that the groove resembles the reduced thickness of modern platyrrhines. This provides fossil corroboration of the hypothesis originally based on living species, that the last common ancestor shared by platyrrhines and catarrhines was already less reliant on the sense of smell than a strepsirhine primate.

These critical fossil finds have demonstrated that platyrrhines are the more primitive of the two lines of extant anthropoids in some traits. It suggests that living platyrrhines, rather than the Old World monkeys or apes, should be used to model the behavior and adaptations of these early Old World anthropoids. *Aegyptopithecus zeuxis* is a good example in its postcranial traits as well as in the cranial morphologies mentioned. Its elbow morphology and limb proportions do not resemble any Old World monkey or ape, but very closely resemble a platyrrhine, the Howler Monkey. This indicates that in life *Aegyptopithecus* engaged in a style of locomotion that was very different from that of any living Old World anthropoid, but would have resembled the deliberate form of quadrupedalism seen in howlers. Another example is the skeleton of the small Egyptian fossil *Apidium phiomense*. It closely resembles the Squirrel Monkey rather than any of the Old World monkeys, indicating it used leaping in its locomotor repertoire. Various other examples involve similarities between early

African forms and platyrrhines in the functional morphology of the dentition. The modern platyrrhines are thus a living laboratory for testing hypotheses about the nature of early anthropoid ecology, behavior, and evolution.

### Platyrrhine taxonomy

The taxonomy of platyrrhine genera and species, their identification and arrangement in classification, remains a subject of some debate among scholars. The 16 living genera recognized and discussed in this book are based on the work of myself and many others, involving intensive study of the morphology of all the living platyrrhines at the genus level, and studies of the taxonomy, behavior, and ecology of species contained in each genus. This count has been a relatively conventional and stable figure since about 1925; however, there has been an accelerating trend since 2000 to re-taxonomize platyrrhine genera and species based almost exclusively on molecular studies, and now more than 20 genera are recognized by some.

Even more controversial is the number of platyrrhine species. CITES, the Convention on International Trade in Endangered Species of Wild Flora and Fauna, an authoritative organization that tracks biodiversity, listed 146 living platyrrhine species in 2018. *The Handbook of Mammals of the World. 3. Primates*, a 2013 landmark treatment of primate biology written by active field biologists and conservationists, identified 156 species. In contrast, *Mammal Species of the World*, a comprehensive text organized by the Smithsonian Institution and written by experts in the taxonomy of each mammalian order, recognized 85 platyrrhine species in 1993, and fewer than 50 species were presented in 1976 by P. H. Napier, a pioneering primate specialist who was then writing catalogs covering all the primates housed in the research collections of the British Museum.

The progression from roughly 50 to more than 150 species did not occur because we discovered more than 100 new species between 1976 and 2018 that had been hidden in the jungle; perhaps there were a handful. It happened because different approaches were being employed by the scientists working on the taxonomy of species and genera, in the evidence used, and in the conceptual models they applied to species and genera, which will be discussed in later chapters. An example of how this new methodology changes things is the taxonomic status of Titi Monkeys. Over a 60-year period ending in 2016, three separate scientific revisions of the classification of titis variously concluded that there are 3 species, 13 species, or 34 species. Though it was long accepted that all titi monkeys constitute a single genus, *Callicebus*, the authors of a 2016 study felt the need to organize the species into three genera instead of one.

There are consequences to this strategy, which has been called taxonomic inflation, an artificial increase in the perceived number of species and genera in nature. It begins with a question of credibility, because none of the research done with this approach has ever reduced the number of species in a multispecies genus, as might be expected when powerful DNA methods are applied to sort out any taxonomy involving many populations. Instead, the taxonomic standing of monkey populations previously classified as subspecies has been elevated to the rank of species, which changes the biological significance of their names but does not actually alter our knowledge of their existence, as if they had not been previously discovered in nature. As to the significance of such changes to a research program, flattening the species confounds a very basic theoretical tenet of evolution, that variation *within* species is what provides the material basis for potential species change. Taxonomic inflation has the effect of homogenizing the perceived variability within species by eliminating the geographically distinct subspecies divisions whose smaller size and spatial distribution can encourage genetic isolation, for example, an early step in the evolution of fresh traits that can transform populations and generate new species.

Another repercussion of the taxonomic inflation trend is that different, incompatible methods are being applied to document biodiversity and classify living and fossil primates. This is not only a matter of theoretical interest. Lack of a consistent method of recognizing and classifying living and extinct species undermines the fundamental way we inventory biodiversity. Such difficulties extend to the challenge of reconstructing what happened during the course of evolution, too. They make it virtually impossible to investigate the possibility that nominally extinct species evolved into extant species.

One reason for this radical taxonomic shift since 2000 is that the concept of species has always been difficult to define scientifically, and while it has changed over time, it is likely to remain problematic because of ambiguity. In *The Origin*, Darwin wrote, "No one definition [of species] has yet satisfied all naturalists, yet every naturalist knows vaguely what he means when he speaks of species. . . . Nor shall I here discuss the various definitions which have been given of the term species."

Since Darwin's time, we have tried to develop what we call an operational definition of species applicable to living and extinct forms by identifying natural, universal biological properties. Seen through the prism of evolution, the aim is to apply a formula that integrates biological knowledge about the extraordinarily varied lives and circumstances of organisms like animals in a replicable, yet elastic, way as species are formally recognized by science.

By the 1930s, scientists understood that the species is a fundamental unit of evolution and it was proposed that the fundamental property of a species is

exclusivity of reproduction. The biological species concept became the dominant paradigm. Its most widely accepted definition was given by the eminent 20th-century evolutionary biologist and ornithologist Ernst Mayr, who in 1942 explained that species are groups of populations in nature whose members mate with their own kind, act accordingly, and are thus isolated from other such groups.

However, it is very difficult—impossible for the vast majority of cases—to actually test for interfertility between two potentially distinct living species, even more so for the extinct ones. Many have seized on this methodological dilemma, making it a principal reason for discarding the biological species concept and replacing it with the idea that species are lineages, which is a phylogenetic concept typically applied to higher taxonomic groups. Therefore, in order to operationalize the biological species concept, researchers understood that species are, in effect, distributed networks of reproductively compatible individuals having unique combinations of genes that are likely to be manifest or mirrored in morphology or behavior, as a design.

Subspecies can be thought of as a spatial array of nodes that are connected via the network. That means we can recognize species by finding specific morphological and behavioral patterns that are known or thought to be genetically based, and sufficiently distinct so as to inhibit crossbreeding with another species at any of the subspecies nodes. The indirect evidence that interbreeding is unlikely to happen may come from genes, body proportions, craniodental anatomy, coat color, mating rituals, vocalizations, and more, any combination of important traits that sets two species-like entities apart in a statistical sense and, when observable, in nature. When it comes to comparing fossils that may belong to two distinct species, we apply empirically developed observations of living relatives as a yardstick to delimit interfertility, theoretically.

As mentioned, the taxonomy of platyrrhine genera is also a matter of debate. In some cases this reflects different views of the genus concept, which is not the same as the dispute over the meaning of species. It is generally agreed that species are real entities in nature, each with a unique genetic template and each one being an individual, direct product of evolution. The genus, in contrast, is not a real thing in nature. There is no natural process that produces a genus per se. It is a construct utilized by scientists to aggregate species that are identified by a uniquely shared phylogenetic and adaptive origin that establishes a unique ecological position for the collective. There are no direct or indirect tests, as there might be for species no matter the difficulty of applying them. That is why classifying at the genus level is a subjective process. In cases where a genus comprises only a single species, the factors determining its taxonomic status as a species are the same as those identifying it as a

genus. Two such examples are presented in the next chapter, concerning the Pygmy Marmoset and Goeldi's Monkey. They reveal another practical difference between classifying at the species level and the genus level. There is no unifying criterion that determines their taxonomic status, like the breeding standard. Different details are used to define each genus because each one is adapted differently; that is, body size may be construed as a primary genus-level character in one instance and craniodental morphology may be the defining character in another. Another example involves the current controversy regarding the number of genera representing capuchin monkeys, also discussed below.

Why does the actual number, or the best scientific estimate, of genera and species of New World monkeys matter? Because these classifications tell us different things. To study the fine points of evolution is to study species. Natural selection, the universal process by which traits benefiting reproductive success are preserved over generational time, among other factors, acts on individuals, and their genetic contribution to a larger population, to the species, is what determines what features will change or remain the same. Thus it matters greatly to be able to properly identify species. To study the structure of an adaptive radiation is to study genera, what constitutes each genus and how many genera there are. The genus is the taxonomic level at which we can trace the distinctive pattern of platyrrhine evolution, which comprises many multimillion-year lineages of genera and monophyletic collections of genera.

The formal taxonomic names for the 16 living platyrrhine genera used in this book are the established ones employed for many decades, and are italicized according to nomenclatural rules. The informal names are not subject to the same conventions and have varied over the years, but they are capitalized as the name of a genus. Therefore, as an example, the name Squirrel Monkey is capitalized when it refers to the genus *Saimiri*; the lowercase squirrel monkey is used as a generalization.

## 20 million years of evolution

### 16 genera of extant platyrrhine primates

Genus-level descriptions of each of the living platyrrhine primates are presented in the following chapter. The genera recognized in this book have been identified as such for decades, although there have been a few cases where a species has been moved from one genus and placed into a different one. The Pygmy Marmoset is an example. It is generally agreed now that this one living

species is different enough from all other platyrrhines to warrant placement in a genus of its own, *Cebuella*. In the past, however, some, including the present author, preferred to place that single species elsewhere, classifying it with other types of monkeys in the genus *Callithrix*, a group of monkey species with overlapping adaptations.

In studying how living primate genera are situated ecologically, the most important characteristics are body size, diet, locomotion, the brain, activity cycles, reproductive patterns and behaviors associated with social organization, and mating strategies. Some of these features can also be examined in the fossil record in various ways, which amplifies the importance of understanding them. They are introduced in chapter 2, and other details concerning the evolution of these traits as adaptations are further discussed in subsequent chapters. In most respects the characteristics that provide the basis for recognizing platyrrhine genera are the same kinds of traits that delineate genera in the larger world of mammalogy.

Body size, diet, locomotion, cognition, and social behavior are examples of adaptive complexes that are all linked biologically at several levels. Still, in the analysis of what makes an animal successful, even a single trait or complex can be highly informative. It may set a genus apart from its relatives for purposes of identification and also serve as a primary correlate or building block with respect to other traits that support a given lifestyle. For example, in pygmy marmosets a tiny body size—adults rarely weigh more than 120 g, roughly 4 oz—enables the animals to subsist on an unusual diet that includes large amounts of natural gum that exudes from trees. Locally, this diet reduces feeding competition with other platyrrhines and it also minimizes a pygmy marmoset's daily energy output by saving it the expense of searching widely for other foods.

Specialized incisor and canine teeth enable these very small monkeys to access gums by scraping away patches of tree bark. The tree responds by forming a dribble of gum to heal the wound. Coupled with these features are postural adaptations of the skeleton and especially the fingers and toes that allow the monkeys to position themselves on trees so gouging can be done effectively. A practical benefit of the constellation of adaptations is that an entire family unit of pygmy marmosets may be able to subsist for long periods of time by feeding on a single tree that is rich with gum, as long as the tree can survive the onslaught of daily hole-gouging to stimulate the production of gum globules. When life revolves around a single tree, a limit is placed on home range and social group size, and a premium may be placed on territorial behaviors in defense of one, highly valued food resource.

A tiny body size is the adaptive cornerstone of the pygmy marmoset's existence. The coordination of adaptive systems involving food, movement, and interpersonal and intergroup behaviors with body size in *Cebuella* is comparable to the adaptive paradigms seen in every other platyrrhine genus, making each one unique. Body size is more than a descriptor. It is a fundamental design element governing an animal's lifestyle and evolutionary history, and it is strongly influenced by natural selection. As we shall see, there are platyrrhines 100 times larger than the Pygmy Marmoset, such as the largest Spider Monkeys and the Muriquis, and their body size plays a similar role in defining their lifestyles. In historical terms, this extensive range of body sizes is not a continuum. Rather, in reconstructing the evolution of platyrrhines it becomes apparent that different clades and genera have experienced different trajectories of body-size evolution. Some have gotten smaller and some have gotten larger over time. Even though it is difficult to accurately infer the magnitudes of these adaptive shifts, it is evident that, comparatively, some forms are phyletic dwarfs and others are phyletic giants.

In reconstructing the evolutionary history of platyrrhines it also becomes clear that the radiation of New World monkeys as a group is characterized by a preponderance of long-lived individual genera, generic lineages, and clades. A generic lineage can be thought of as a line of descent or a stream of genes effectively evolving in a column that produces a coherent set of characteristics that determine the unique ecological lifestyle shared by all its descendants. The genetic column may involve a fossil species that bears the same genus name as a living genus, as with a 12–14-million-year-old fossil Owl Monkey and its living counterpart, both named *Aotus*. Or, a generic lineage may involve two differently named genera that are separated by a significant amount of geological time, but they are monophyletically related and fall within the same lifestyle boundaries. In other words, while the anatomical evidence may make it too much of a stretch to hypothesize that the species of the older genus is a direct ancestor of a species belonging to the younger genus, the former is considered directly in or near the ancestry of the latter because the morphologies align, their temporal ages are consistent with the idea, and that hypothesis is not discounted by relevant evidence. We can infer the longevity of genus-level lineages through the fossil record and by using molecular methods which help us reconstruct how genera are linked up with one another cladistically, and when the splits between and among the branches of the platyrrhine Tree of Life occurred.

A half-dozen or more of the 16 living platyrrhine genera can be traced back to fossils, as genera or generic lineages, that date between 7 and 20 million years. The implication is that these living genera have remained much the

same as they were millions of years ago, in the body parts that have been discovered in fossils. Furthermore, insight about how modern platyrrhines are organized locally tells us that these genera evolved in connection with one another, enabling them to coexist in harmony within the same community by occupying unique niches within an ecosystem. Having such a high proportion of genus-level lineages representing most of the major phylogenetic clades of living New World monkeys over such a long time interval reveals that platyrrhine history has proceeded in a pattern, as a unified radiation rather than an evolutionary venture that produced a chaotic ensemble of primates. There is plenty of unpredictability in the evolutionary process, but the manner in which the modern platyrrhine radiation unfolded was anything but random.

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