MARTIN MOYNIHAN

The New World Primates

Adaptive Radiation and the Evolution of Social Behavior, Languages, and Intelligence

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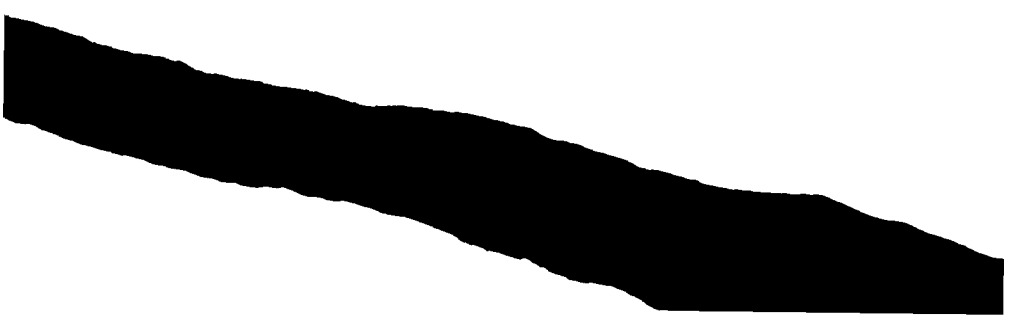

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For my wife

Contents

Preface

There have been so many books on primates—monkeys and apes and their relatives—in recent years that one hesitates to produce yet another. It would seem that some justification is called for. Perhaps the only valid excuse is that primates are particularly interesting. They are, or should be, interesting for several reasons.

Man himself is a primate. He is descended from something that would be called an ape were it still living today. Apes are descended from animals that would be called monkeys were they still living today. One would like to know and understand the factors that have influenced or controlled the changes from one stage to another.

The monkeys of Central and South America may be relevant in this connection, although in a rather peculiar way. They are not very closely related to the immediate ancestry of man, which developed from one of the stocks of Old World primates. Certain anatomical details would indicate that they are less closely related to the monkeys and apes of the Old World than the latter are to one another. Yet they seem to have evolved many of the same characteristics independently, probably several times. They also are abundant and rather diverse. Thus, they provide unusually favorable opportunities for analysis of both evolutionary radiation, the appearance of new adaptations to new manners of life, and repeated convergence in similar physical and biological environments.

My qualifications for reviewing them consist of some sixteen years of intermittent observations of many species in captivity and in the wild. Six types were studied with some degree of thoroughness: *Saguinus geoffroyi, Cebuella pygmaea, Aotus trivirgatus, Pithecia monacha, Callicebus moloch,* and *Saimiri sciureus.* Additional forms of some of the same genera and one

or more representatives of all the other genera (and a majority of distinctive subgenera) were observed more briefly. I have also relied upon the published reports of other students and verbal information from both professional scientists and non-technical observers in the field. I must thank these informants and hope that I have not distorted their accounts unduly.

Every author has preferences and biases. My own will be evident. I have been most concerned with patterns of social behavior and some interactions among individuals, and I have tried to trace their development in their historical and ecological contexts. This book is not meant to be a comprehensive or "balanced" summary of the whole of the biology or even the ethology of New World primates; rather it is a series of descriptions and discussions of special topics that seem to me to be significant, suggestive, or amusing.

The task of preparing and writing up the material was facilitated by much editorial, bibliographic, technical, and secretarial advice and assistance. I am particularly grateful to the secretaries, who must have been driven to distraction by the nature of the texts with which they had to work, and to Mrs. Alcira Mejía, Mrs. Bernadette French, and Mr. Jack Marquardt of the Smithsonian libraries.

Mr. John Hannon, of the Princeton University Press, was always encouraging as well as helpful.

The editors of the Smithsonian Institution Press and the *London Journal of Zoology* kindly gave permission to reproduce some of the figures.

I am indebted to the Smithsonian Institution itself for having provided me with so many opportunities for research.

Primatology is changing and progressing, and any review may become obsolete. I should, therefore, specify the time of my comments. A draft of this book was finished in September of 1973. Changes and additions were made later, in 1974.

MARTIN MOYNIHAN

Panama City, the Republic of Panama

Infant Callimico goeldii.

chapter one

NOTES ON CLASSIFICATION AND HISTORY

The Order Primates

Most primates are easy to recognize as such, but the recognition usually is based upon unconscious assessment of data that are difficult to describe or summarize concisely.

The classical definition of the order was by Mivart (1873): "Unguiculate, claviculate, placental mammals, with orbits encircled by bone; three kinds of teeth, at least at one time of life; brain always with a posterior lobe and calcarine fissure; the innermost digit of at least one pair of extremities opposable; hallux with a flat nail or none; a well-developed caecum; penis pendulous; testes scrotal; always two pectoral mammae."

Unfortunately, this definition is neither all-inclusive nor very useful. Many characteristics of soft anatomy are not evident in most fossils. More important, there are several species, living or extinct, that have always been considered to be primates although they lack some of the characters cited by Mivart.

Another problem was noted by Huxley (1876). Surveying the primates as a whole, he said that "Perhaps no order of mammals presents us with so extraordinary a series of gradation 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 mammals."

Recent discussions have used more sophisticated terms, but are not necessarily more helpful. To mention one example, Martin (1968a) has suggested that primates can be identified by a rather recondite character of the bony skull, central nervous system, and reproductive organs. He is not certain, however, that any of these features are diagnostic per se. Moreover some of them would appear to bear little or no causal relation

to the adaptations that have been responsible for the greatest successes of the order.

It may be prudent, therefore, to be vague. For most practical purposes, primates can be described simply as placental mammals primarily adapted to arboreal life, usually eating a variety of foods, and with more or less grasping hands and feet, large and complex brains, and binocular vision.

Even this must be qualified by exceptions. There are primates that spend (or may be supposed to have spent) all or most of their time on the ground. But they show unmistakable signs of being related to or descended from (sic) arboreal forms.

Whatever the difficulties, most people would agree that the living primates include the following:

1. Lemuroids. Many species of the island of Madagascar, the "true" lemurs and some more exotic animals.
2. Lorisoids. The lorises of southern Asia and the galagos and pottos of continental Africa.
3. Tarsioids. Several species of the genus *Tarsius*, confined to the Philippine and other East Indian islands.
4. Ceboids. The native primates of the New World, apart from man.
5. Cercopithecoids. The guenons, mangabeys, macaques, baboons, langurs, guerezas, etc. of the Old World. They range through most of continental Africa, large parts of Asia, and some nearby areas such as Gibraltar and Celebes.
6. Hominoids. Man and the "great" apes, including the gibbons, Siamang, and Orang-utan of southeast Asia, and the chimpanzees and Gorilla of Africa.

These groups have been assigned different ranks, arranged in different ways, by different specialists. Simons (1972) provides an authoritative recent classification, to the generic level, of both living and fossil primates, and also cites checklists by other authors. Two major supergroups are obvious.

The lemuroids, lorisoids, and tarsioids appear to be less specialized or "progressive" than the other living primates in some respects. With their fossil relatives, they usually are placed together (following Simpson, 1945) in a separate suborder, the Prosimii, and given the "vernacular" name of prosimians.

The other groups are usually bracketed in a suborder Anthropoidea. Most of the ceboids and cercopithecoids are called monkeys. By "monkey" the layman usually means a moderately large primate, comparatively intelligent, disconcertingly manlike in some aspects of behavior, but with a visible tail. This is as good a definition as any, although somewhat misleading in a few special cases. By "ape" the layman who speaks a language, such as English, that distinguishes among different types of primates usually means something very like a monkey, but probably even larger and certainly without a conspicuous tail. Biologists who use the term usually restrict it to Hominoids apart from man.

Terms such as "intelligent" and "intelligence" are also difficult to define. I shall not attempt to analyze the various concepts that might be involved. It will be sufficient to say that the terms are being used in the ordinary, everyday sense. In effect, this means that intelligence is equated with ability to learn new things and to apprehend relations between perceived phenomena. (For a discussion and summary of some of the ways in which the term "learning" has been used, see Thorpe, 1956.)

Of course, it is impossible to test the intelligence of extinct animals. And really very little is known of the learning abilities of some of the living primates. But this is not quite as serious a handicap as might be supposed. Among those animals whose behavior has been studied in the laboratory or in other controlled situations, there has been found to be a general positive correlation between size and superficial complexity of brain and intelligence. Small animals usually have relatively larger brains than otherwise similar large animals. Among spe-

cies of similar body size, however, the forms with larger brains usually prove to be more intelligent than those with smaller brains. At any given size, mammals whose cerebral hemispheres are convoluted on the surface tend to be more intelligent than those with smooth brains; and convolutions may make impressions upon the inner walls of the cranium. Thus morphology alone, the size, shape, and other aspects of the skull, can be used as a crude gauge of intelligence. (Comparative aspects of relative brain size and development are discussed in Rensch, 1956 and 1960, Bauchot and Stephan, 1966, Stephan, 1967 and 1972, and Jerison, 1973.)

The Earliest Primates

As indicated above, some of the primates are quite similar in basic anatomy to the most primitive of placental mammals. The latter are conventionally placed in the order Insectivora. The tree shrews (family Tupaiidae) would seem to be the most nearly primitive of living Insectivora. It is not coincidental that they were also at one time considered to be the most primitive of living primates. This opinion is now unfashionable (see, for instance, Van Valen, 1965, Campbell, 1968, and Martin, 1968b), but it seems probable that the first primates cannot have been very different from tupaiids in either behavior or ecology.

Living tree shrews are confined to tropical Asia. They are small animals of not very distinctive appearance (remotely similar to squirrels, ordinary shrews, or opossums) with rather small brains. They have been studied almost exclusively in captivity, but thoroughly enough to give some idea of their normal activities. The best known forms, possibly all subspecies of *Tupaia glis*, seem to be diurnal, nearly omnivorous, and partly terrestrial and partly arboreal (Kaufmann, 1965, and Martin, 1968b). They use their hands for grooming and occasionally holding food, despite a primitive arrangement of fingers that is not particularly suited to the more complex or delicate kinds of manipulation (Bishop, 1962 and 1964).

Adults are not very gregarious, but they have a fairly extensive repertory of social signals. They seem to have more different types of patterns that have become specialized for communication than other shrews, but less than all or most typical primates (Moynihan, 1970a). Many other species of the family Tupaiidae seem to be essentially similar. A few may be slightly more highly social, more frequently or extensively gregarious (Sorenson and Conaway, 1966).

Starting from some such source, the true primates developed at the end of the Cretaceous period and the beginning of the Tertiary period, approximately 70 to 65 million years ago (Van Valen and Sloan, 1965, McKenna, 1966, Szalay, 1967, Simons, 1963, 1964, 1972). Presumably the adaptive shift involved an increase of arboreality and a greater reliance upon vegetable foods. (The precise sequence of changes is not entirely clear, and there may have been additional factors at work—see Cartmill, 1974a—but the general trend is unmistakable.) All the earlier primates can be called prosimian. They seem to have become extremely varied between the middle Paleocene and late Eocene epochs, perhaps 60 to 34 million years ago. Many of the Paleocene types were rather surprisingly rodentlike, even more so than tree shrews, with procumbent and gnawing front teeth, but most of the better known Eocene species were more nearly comparable to the modern lemuroids and tarsioids.

Of the surviving prosimians, only the lemuroids are flourishing enough to suggest the probable range of habits of their earlier relatives. They will be described in some detail in Chapter 6, but a few points may be noted here in anticipation. The living species are both more varied than tree shrews and more specialized on the average. They are small to medium large in size. Some are diurnal. Others are nocturnal. They all eat vegetable matter. A few also take insects and other small arthropods, which they may catch in different ways. Some species and subspecies are highly gregarious, living in large bands that include several adults of both sexes. Others live in apparently

stable family groups of one adult male and one adult female with their most recent young. Still others are often solitary. All of them have more or less elaborate signal systems. The great majority of the species are arboreal. They have hands and feet that are better adapted to grasping than are those of tree shrews, but they seem to use the increased capability primarily for locomotion, seizing trunks and branches of trees and bushes, rather than for manipulation of other objects (A. Jolly, 1966).

Although the brains of most living lemuroids and tarsioids are proportionately smaller and apparently simpler than those of living monkeys, they are more highly developed than those of tree shrews and they are not relatively small in comparison with the brains of most living mammals of other orders. What little evidence there is indicates that Eocene prosimians had brains like those of their present day counterparts (perhaps with more emphasis on olfaction, the sense of smell, in some cases). As most other Eocene mammals had much smaller brains than their nearest living relatives, this would seem to mean that the early primates were already the most intelligent of contemporary animals. See also Radinsky (1970). It is interesting, and must be significant, that the primates had already acquired this advance or advantage at the prosimian stage.

The Eocene prosimians, in turn, must have given rise to all the "higher" monkeys and apes, including the forms that are now found in Central and South America.

The Ceboids

The monkeys of the New World have often been divided among a host of taxonomic categories, families, subfamilies, tribes, etc., with a corresponding proliferation of complicated and unstable names. Some of this effort seems to have been sheer embroidery or hairsplitting. The living forms fall naturally into some eight or nine subgroups. I would suggest that they be listed as follows:

1. Tamarins. Genera *Callimico*, *Leontopithecus*, and *Saguinus*.
2. Marmosets. *Callithrix* and *Cebuella*.
3. The Night Monkey or Douroucouli. *Aotus*.
4. Howler monkeys. *Alouatta*.
5. Sakis and uakaris. *Pithecia* (including "*Chiropotes*" and "*Cacajao*").
6. Titi monkeys. *Callicebus*.
7. Spider monkeys and the Woolly Monkey. *Ateles* (including "*Brachyteles*") and *Lagothrix*.
8. The Squirrel Monkey. *Saimiri*.
9. Capuchin monkeys. *Cebus*.

Most of the scientific names in this list conform to Hershkovitz (see below). Names in quotation marks are traditional in the literature, but the taxa to which they have been applied do not, in my opinion, deserve to be recognized as separate genera. Many resemblances between taxa can be conveniently shown by setting broad, inclusive generic limits. The classification proposed and used here favors "lumping" over splitting as a general rule.

The limits and contents of the subgroups have been determined by studies of extant animals. In the circumstances, it is impossible to arrange them in any clear linear sequence or hierarchy. With one or two exceptions, each subgroup appears to be almost equally distinct from every other. Similarities and differences are distributed in complex patterns.

It would also be difficult to establish that any one of the subgroups is conspicuously more primitive on the average than several others. Most of them exhibit an array of both obviously specialized and primitive features of morphology and behavior. (Hershkovitz, e.g. 1970 and 1968, suggests that the small tamarins and marmosets are primitive among the living forms, and that the smallest, *Cebuella*, is the most primitive of all. This is debatable. It is true that many early primates were small. But

the size of tamarins and marmosets, and many other characters that seem to be functionally related, are directly adaptive. They could be "secondary" specializations. They certainly are combined with progressive features.)

There are enough resemblances among ceboids to indicate that they are monophyletic. The immediate common ancestor is not known, or at least has not been recognized and definitely identified as such. It may have already advanced beyond the prosimian stage toward the monkey level.

The courses of evolution of particular lineages of New World primates are obscure. They do not, as monkeys, have a good fossil record. The earliest traces of unmistakable ceboids are of Oligocene and Miocene ages, some 34 to 12 million years ago, and were found in South America. South America was an island during all or most of the Tertiary, and the home of a most peculiar fauna of mammals, birds, and other vertebrates (Darlington, 1957, and Patterson and Pascual, 1968 and 1972), some of which have survived to the present day, others of which have not. The ceboids were and are among the diagnostic members of this fauna. They would appear, however, to have reached South America, or expanded within it, at a later date than some other kinds of mammals (see Hoffstetter, 1972, as well as Patterson and Pascual). The published accounts of the Oligocene and Miocene types are difficult to interpret and to reconcile with one another. Stirton (1951) thought that these animals were near to some of the living forms. Hershkovitz (1970) suggests that most of them were more distinctive, representatives of lines that have not survived. In any case, it is evident that the ceboids had become diversified by the end of the Miocene. The remains of monkeys discovered in late Pleistocene or younger deposits on the mainland of South America, only a few thousands, or tens of thousands, of years old, are nearly or completely indistinguishable from the corresponding parts of living animals.

A few ceboids occur in Central America, essentially the tropical part of North America, at the present time. Tropical cli-

mates and habitats must have been more extensive in the region during some earlier periods. Doubtless they would have been suitable for monkeylike primates. An enigmatic fossil monkey, *Xenothrix*, has been found in Jamaica (Williams and Koopman, 1952). Apart from this, there are no indications that Central America or tropical North America could have been the site of a major or independent evolution of ceboid groups. The monkeys that occur there now are recent immigrants (see also below). South America is the home of the successful ceboids, and their basic adaptations are to South American conditions.

chapter two

THE SETTING

The physiography of South America is simple in broad outline, with the high chains of the Andes to the west, older and lower mountains in parts of the east, and extensive lowlands in the drainage basins of the great rivers, the Magdalena, Orinoco, Amazon, Paraná, and others. The area is approximately 11,200 square kilometers. A very substantial proportion, perhaps 75 per cent, lies between the tropics of Capricorn and Cancer. (Figures taken from Keast, 1972a.)

The bulk of the tropical area is lowland. At the present time, much of it is covered by different kinds of forest and scrub, including rain forest. Under "natural conditions," that is, present climates and no interference by man, the areas of forest and scrub in general, and rain forest in particular, would be considerably larger. Rain forest is the richest and most diverse of plant formations in the sense of being composed of a multitude of species of very different shapes and sizes (Richards, 1952 and 1973b, and Parsons and Cameron, 1974). As would be expected, the fauna that lives there is also exceedingly diverse, more so than in any other terrestrial habitat.

This system probably has existed in South America for a very long time, although not without variations. There certainly have been climatic vicissitudes, alternate periods of relatively greater and lesser humidity, especially during the Pleistocene (see summaries and references in Simpson Vuilleumier, 1971, Vanzolini, 1973, and Raven and Axelrod, 1974). Students of birds (Haffer, 1967, 1969, and 1974) and lizards (Vanzolini and Williams, 1970) have argued that the humid forest must have been repeatedly broken up into separate pockets or patches, "refugia," during drier periods. They have also suggested that the process contributed to the multiplication of species in the tropics. Originally similar populations of forest

organisms may have become differentiated during the stages of fragmentation. They could have developed divergent ecological preferences and potential reproductive isolating mechanisms. These, in turn, might have permitted their descendants to coexist without interbreeding when the various patches spread and coalesced again during wetter periods. See also Mayr (1969).

This phenomenon would seem to be real; but its effects may have been limited or small scale in the lowlands of tropical South America. The best evidence that forests have been predominant throughout the history of tropical South America is that most of its fauna is adapted to forested conditions. It includes relatively very few open country or savannah types (Vesey-Fitzgerald, 1964, and Hershkovitz, 1969 and 1972).

There are savannahs in parts of lowland, tropical South America now. Their origin is a matter of some dispute (points of view are presented in Beard, 1953, Goulissachvili, 1964, Talbot, 1964, and Vesey-Fitzgerald). It seems probable that most of them are artificial, the products of comparatively very recent human activities.

Tropical America would seem to have escaped the really severe and widespread aridity that has been characteristic of some parts of the Old World tropics, most notably Africa (Moreau, 1966), during the last million years or so. This may be one of the reasons why its flora is richer than that of tropical Africa (Richards, 1973a). It might also help to explain some of the differences between the ceboids and their Old World relatives (see below).

American monkeys do not betray the effects of having been confined to refugia in the same way or to the same extent as some birds. Different genera of ceboids have different ranges. Some of them include many more visibly distinct forms than do others. In most cases, however, each genus is represented by no more than a single type in any given area. Many other kinds of mammals illustrate the same general rule. Extensive sympatry, i.e., overlapping of ranges, of closely related forms

seems to be much rarer among the larger nonflying mammals of Central and South America (everything "above," in several senses, the rats and mice) than among the birds of the same areas or comparable mammals of other continental masses of similar latitudes, such as Africa and southern Asia. This must mean that they have had fewer opportunities to speciate in geographic isolation. (Possibly the periods of reduction and shattering of rain forests were only brief episodes in the New World tropics and/or the shattered fragments were still connected by corridors of more open forest or scrub that were not prohibitive barriers to larger mammals, whatever their effects upon other organisms.)

There must also have been biological and zoogeographical changes of different magnitudes and on very different time scales.

It has often been assumed that the tropics are "stable." The statement is misleading as a generalization, although not always in detail. There are appreciable fluctuations in population numbers and distributions from year to year and decade to decade in humid forests and elsewhere (personal observation—see also comments in such works as Eisenberg and Thorington, 1973). It is even possible that changes in tropical biotas and environments are more unpredictable in the short run or in some respects than are those of the north temperate zone. May (1972 and 1973) discusses, with a wealth of mathematical formulas, some of the relations and conditions that might favor instability in complex systems. To put it crudely, the choice is between correction by homeostasis, feedback mechanisms, and disturbance by domino effects in chain. Obviously both have occurred (MacArthur, 1972). More important, in fact, are the unmistakable and undoubted revolutions that have succeeded, as connections among land masses, plates, and continents, have shifted over the longest relevant time span, the last few tens of millions of years.

The present faunas of South America, Central America, and the West Indies are mixtures. They include elements that

evolved in North America and in South America when the two continents were separated during the Tertiary and that later strayed out to the islands or migrated north or south along the mainland when a connection was (re)established in the vicinity of the isthmus of Panama and northern Colombia in the late Pliocene or early Pleistocene. Today the three areas and the various mixtures are usually considered by zoogeographers and other biologists to form a single "neotropical region." All the warm, lowland continental and isthmian parts can be included in a single subregion. This may be called "Brazilian," following Hershkovitz (1958). The most conspicuous division within it, at the present time, is imposed by the Andes. These separate some of the organisms of the Amazon and Orinoco basins from those of Central America and the Pacific coast of Colombia and Ecuador. But the mountains have not been a complete barrier, and many of the animals and plants are quite similar on both sides. Only the biota of the upper Amazon valley is somewhat more variegated, possibly because physical conditions are somewhat more favorable there.

The actual components of the modern neotropical mammalian fauna are described by Hershkovitz (1972), summarized and analyzed by Keast (1972b), and also by Eisenberg and Thorington (op. cit.). They include 12 orders (perhaps 24 taxa at the combined ordinal and superfamily grades), 50 families, 278 genera, and approximately 810 species. (The figures for genera and species may well be overestimates.) The dominant groups, in terms of numbers of species, biomasses, and trophic levels, are monkeys, bats (Chiroptera), rodents (cricetine rats and mice, and the caviomorphs, some of which are ungulatelike, others of which are tree-living), opossums (didelphid marsupials, often arboreal), edentates (tree sloths, anteaters, armadillos), placental Carnivora (also often arboreal), and real ungulates (deer, tapirs, and peccaries in the tropical parts of the region). The mammals that are most likely to impinge upon monkeys as possible competitors are

some of the opossums, the tree sloths, and some of the rodents, squirrels, and porcupines.

It may be revealing to consider one of the past cases of replacement in the neotropics. Placental carnivores are occasional predators of at least a few of the New World primates at the present time. This is interesting because the only mammalian predators in South America during most of the Tertiary belonged to a different and now extinct group, the borhyaenid marsupials. It is remarkable that the ceboids have been able to withstand an extensive changeover of a large series of predators (and not all that long ago) without more apparent damage. Although predation may be important in particular instances, and must have been one of the factors affecting the evolution of ceboids, it may not usually be the principal cause of mortality among them. All or almost all of the extant species take precautions against predators, sometimes elaborate precautions that are exceedingly visible to the biologist, but the majority of individuals may die from less visible causes, such as old age, malnutrition, and disease. (There are indications that predation is often *relatively* less important in the tropics than in some other regions—Moynihan, 1971.)

Other arboreal herbivores and omnivores, such as tree sloths and some opossums and rodents, would seem to have withstood the same change of predators with equal success. Perhaps some aspects of the arboreal habitus and habitats are as nearly imperturbable as other parts of the tropics are supposed to be?

Conservative or not, primates and other mammals have always had to cope with other organisms of different classes and even phyla. Birds are one example; South America has a superabundance of them. De Schauensee (1970) recognizes 93 families, 865 genera, and 2926 species. This is by far the richest assemblage of birds in the world (it is approximately twice the size of the avifauna of Africa). Much of it is tropical and occurs in forests. A few species of birds are predators