

---

# ECOLOGY AND BEHAVIOR OF NEOTROPICAL PRIMATES

---

## VOLUME 1

*Edited by:*

Adelmar F. Coimbra-Filho  
Coordenador, Centro de Primatologia do Rio de Janeiro,  
DECAM - FEEMA

Russell A. Mittermeier  
Chairman, IUCN/SSC Primate Specialist Group; and Director, World  
Wildlife Fund - U.S. Primate Program

Academia Brasileira de Ciências  
Rio de Janeiro, 1981

ERRATUM AND ADDENDUM

Page 9, line 9 ...1812 for 1912

10, line 9 insert marmosets after colon

11, last ...italicize Branisella

12, legend ...to for at

13, Hill, 1957-1962 ...Dolichocebus is misspelled

13, Romer, 1966 ...add " after "fossil

13, Simons, 1972 ...end of classification should read--  
Callitrichidae  
Callithrix, Saguinus  
Xenothricidae  
Xenothrix  
Ceboidea?  
Branisella

14, Cabrera 1958 ...line gaps below Cebus in unintentional

14, Hershkovitz 1977 ...line gaps below Tremacebinae unintentional

15, AND SUCCESSIVE PAGES ...Figures 1 and 2 (but not the legends) are transposed.  
For Fig. 1 see Fig. 2 and vice versa.

21, 9 from bottom ...of for or

22, 23 ...a colon for the hyphen

22, 9 from bottom ...add a comma after parenthesis

23, 7 ...Few for A

24, 24 ...et al, 1975 for 1976

26, 12 from bottom ... Joysey for Loysey

Rose, K. D. and Fleagle, J. G., 1981, The fossil history of nonhuman primates in the Americas. In: Ecology and Behavior of Neotropical Primates. A.F. Coimbra-Filho and R.A. Mittermeier (ed.s). Academia Brasileira de Ciências, Rio de Janeiro, pp. 111-167.

Rosenberger, A. L., 1980, Gradistic views and adaptive radiation of platyrrhine primates. Z. Morph. Anthropol., 71:157-163.

## Systematics: The Higher Taxa

Alfred L. Rosenberger

*To maintain greatest usefulness, classification must be consistent not with knowledge of some fixed time in the past, but as nearly as may be with the constantly changing knowledge of today. It is, therefore, desirable that classifications should not remain static but should change constantly as pertinent knowledge expands*

G. G. Simpson (1961:111)

### I. INTRODUCTION

Historical reviews of the higher classification of the living New World monkeys have recently been presented by Cruz Lima (1945), Hill (1957, 1960), Napier (1976) and Hershkovitz (1977), and Thorington (1976) has also assessed the "state of the art" of platyrrhine classification at its various taxonomic levels. The purpose of this paper is to present a brief historical account from a somewhat different perspective, and also to provide a synopsis of some of the more influential or historically representative arrangements that have appeared since the first suprageneric classification of the platyrrhines was introduced by E. Geoffroy in 1912. Perusal of these, as well as the many relatively standardized classifications offered by current students, suggests that very little has changed since the middle of the 19th century. This dramatically contrasts with the situation of lower level, alpha taxonomy, which has improved substantially in recent decades (see Mittermeier and Coimbra-Filho, this volume) and has undergone many modifications. If higher level classification, beta taxonomy, is to keep pace with alpha taxonomy, with new data and ideas on the systematics of the platyrrhines and with modern evolutionary principles, then a revised suprageneric classification would appear long overdue.

Along with a review of conventional arrangements, I suggest in this paper an alternative generic classification based upon, and consistent with, a general hypothesis of the phylogeny of New World monkeys and their adaptive radiation. Some of the evidence for the latter has already been presented (Rosenberger, 1977, 1979a, 1979b), and a comprehensive review is now being prepared. A version of the classification offered here, deriving from that work, was given by Szalay and Delson (1979). Since the terminology of my arrangement differs somewhat from that currently in use, I avoid using taxonomic names for suprageneric groups in the first parts of this paper. Instead, the following vernacular terms are defined: (*Callithrix*, *Leontopithecus*, *Saguinus*, *Callimico*); non-marmosets (all the remaining living platyrrhines); saki-uakaris (*Pithecia*, *Chiropotes*, *Cucujao*); spider-woollys (*Ateles*, *Brachyteles*, *Lagothrix*). Except for including the pygmy marmoset "*Cebuella pygmaea*" in the genus *Callithrix* (because I believe that the *jacchus*-group is probably more closely related to *pygmaea* than to the *humeralifer-argentata* group), I accept the same living genera recognized by such authorities as Cabrera (1958), Napier (1976) and Hershkovitz (1977), and the fossil genera recognized by Rose and Fleagle (this volume).

## II. HISTORICAL REVIEW

By convention, the system of hierarchical classification dates back to the tenth edition of Linnaeus' *Systema Naturae* (1758), although he did not use such common taxonomic levels as the family and subfamily. Linnaeus included seven platyrrhine species together with other anthropoids in one genus, "*Simia*", of his Order Primates. These were later allocated to five distinct genera (*Callithrix*, *Saguinus*, *Saimiri*, *Cebus*, *Ateles*) by various students, beginning with Erxleben (1777) who initiated the formal generic segregation of Linnaeus' nonhuman primate species. Except for *Callimico*, which was discovered in 1904, essentially all of the currently accepted living genera were recognized as distinct and formally named by the middle of the 19th century. However, some (e.g. *Callithrix*, *Callicebus*; see Thomas, 1903) presented nomenclatorial problems for more than a century after their original discovery. New World monkey fossils have only become adequately known in the past thirty years, though they were first found near the turn of the century.

According to Hershkovitz (1977) and others, Buffon in 1767 was the first to distinguish between the Old and New World anthropoid primates. However, it was not until the works of E. Geoffroy (1812) and Gray (1821, 1825) that this distinction, as well as intra-platyrrhine suprageneric divisions, became codified and found widespread usage in classifications. As discussed below, the influence of Geoffroy is particularly significant in this regard, but most of the early attempts at higher classification (e.g. Geoffroy, 1812; Gray, 1821; Spix, 1823; Lesson, 1830) drew heavily from the vernacular groupings of still earlier students like Buffon.

Taxonomically, the New World monkeys are usually united as a single group, the Platyrrhini, following the terminology of Geoffroy, and ranked as an infraorder of the suborder Anthropoidea. Simpson (1945), on the other hand, suggested that better taxonomic balance among the anthropoids would be achieved if the New and Old World monkeys and apes were each ranked as superfamilies. In place of the platyrrhine-cathartine dichotomy he used the terms Ceboidea, Cercopithecoidea and Hominoidea, respectively, for the three groups. The terms Platyrrhini and Ceboidea have since been used essentially synonymously by most workers.

#### A) Geoffroy, 1812 -- The Cornerstone of Suprageneric Classification

Most authors (see Tables I, II) have divided the platyrrhines into two major groups, the "Callitrichidae" (marmosets) and the "Cebidae" (non-marmosets). In accordance with the rules of zoological nomenclature, the authorship of these names dates back to Thomas (1903) and to Bonaparte (1831), respectively, although the idea of employing two family groups apparently began with Gray (1821) who, unfortunately, assigned each of his families taxonomic names which proved to be nomenclatorially "illegal". However, it seems that Gray's hierarchical concepts were quite different from those current in the later 1800's, and also from those of modern workers. I infer this because Gray classified his two platyrrhine families in entirely different "Orders", placing the marmosets in an exclusive group and the non-marmosets in a collection that also included the cathartine monkeys and apes, except for *Homo*. Like most subsequent authors, Gray distinguished marmosets from non-marmosets by differences in body size, dental formula, molar shape and the presence or absence of digital claws.

During the 19th century, Hapalidae was the name most frequently used for the assemblage of marmosets. Cebidae was almost universally employed for non-marmosets. The senior synonym Callitrichidae, spelled in many different ways, was shown by Thomas (1903) to have priority over Hapalidae and has essentially replaced it. Many other names have been proposed for subfamilies of non-marmosets but few have been elevated to family rank. (The classifications of Miller, e.g. 1924, provide notable exceptions. He employed five families for the six platyrrhine species inhabiting Central America and no doubt would have been comfortable with several more if only others were able to cross the boundaries he defined for North America). With the discovery of *Callimico* early in the 20th century, and the addition of fossils to the known platyrrhine fauna, the distinction between marmosets and non-marmosets became much less clear-cut and the rationale for maintaining Gray's two-family arrangement came into question. While most workers adhered to it, several have opted for multifamilial schemes. Hershkovitz (1977), for example, employed no less than five families, three for the living species and two for the fossil forms (with an additional family for the fossil *Branisella*, whose taxonomic status he considered indeterminate).

TABLE I

A synopsis of platyrrhine family-group classifications and systematics  
at the generic level<sup>†</sup>

## E. GEOFFROY, 1812

- Helopithecii  
*Ateles, Lagothrix, Alouatta, Cebus*  
Geopithecii  
*Saimiri, Callicebus, Aotus, Pithecia,*  
*Chiropotes, Cacaiao*  
Arctopithecii  
*Callithrix, Saguinus, Leontopithecus*

## GRAY, 1821

- Callitricidae  
1. *Alouatta, Ateles, Cebus, Saimiri*  
2. *Pithecia*  
Hapalidae  
1. *Callithrix*

## SPIX, 1823

- Trichuri  
*Cebus, Chiropotes, Cacaiao, Pithecia,*  
*Callicebus, Saguinus, Aotus, Callithrix*  
Gymnuri  
*Ateles, Brachyteles, Lagothrix, Alouatta*

## GRAY, 1825

- Sariguadae  
Mycetina  
*Alouatta*  
Atelina  
*Ateles, Brachyteles, Lagothrix*  
Callitrichina  
*Cebus* (including *Saimiri*?)  
Saguinina  
*"Saguinus"* (*Lacepede*? = *Callicebus*?),  
*Aotus, Pithecia, Chiropotes*  
Hapalina  
*Callithrix, Saguinus*

## LESSON, 1830

- Helopithecus  
Gymnuri  
*Alouatta, Ateles, Brachyteles,*  
*Lagothrix*  
Trichuri  
*Cebus*  
Geopithecus  
Geopithecus  
*Saimiri, Callicebus, Aotus, Pithecia,*  
*Chiropotes, Cacaiao*  
Arctopithecus  
*Callithrix, Saguinus, Leontopithecus*

## MIVART, 1865

- Cebidae  
Cebinae  
*Ateles, Lagothrix, Cebus*  
Mycetinae  
*Alouatta*  
Pitheciinae  
*Pithecia, Cacaiao*  
Nyctipithecinae  
*Aotus, Callicebus, Saimiri*  
Hapalidae  
*Callithrix*

## GRAY, 1870

- Gymnura  
Mycetina  
*Alouatta*  
Lagotrichina  
*Ateles, Brachyteles, Lagothrix*  
Trichiura  
Cebina  
*Cebus*  
Callitrichina  
*Saimiri, Callicebus*  
Nyctipithecina  
*Aotus*  
Pithecina  
*Pithecia*  
Brachyurina  
*Chiropotes, Cacaiao*  
Hapalina  
*Callithrix, Leontopithecus, Saguinus*

## POCOCK, 1925

- Cebidae  
Aotinae  
*Aotus, Callicebus*  
Pitheciinae  
*Pithecia, Chiropotes, Cacaiao*  
Cebinae  
*Saimiri, Cebus*  
Atelinae  
*Lagothrix, Brachyteles, Ateles*  
Alouattinae  
*Alouatta*  
Hapalidae  
Hapalinae  
*Callithrix, Saguinus, Leontopithecus*  
Callimiconinae  
*Callimico*

<sup>†</sup> This may also include *Saimiri* Voigt, 1831

(cont.)

Table I (Cont.)

## DOLLMAN, 1933

- Cebidae  
 Aotinae  
*Aotus, Callicebus, Saimiri*  
 Pitheciinae  
*Pithecia, Cacajao, Chiropotes*  
 Alouattinae  
*Alouatta*  
 Cebinae  
*Cebus, Lagothrix, Ateles, Brachyteles*  
 Hapalidae  
*Callithrix, Saguinus, Leontopithecus*  
 Callimiconidae  
*Callimico*

## SIMPSON, 1945

- Cebidae  
 Aotinae  
*Homunculus, Aotus, Callicebus*  
 Pitheciinae  
*Cacajao, Pithecia, Chiropotes*  
 Alouattinae  
*Alouatta*  
 Cebinae  
*Cebus, Saimiri*  
 Atelinae  
*Ateles, Brachyteles, Lagothrix*  
 Callimiconinae  
*Callimico*  
 Callitrichidae  
*Callithrix, Saguinus*

## HILL, 1957-1962

- Hapalidae  
 Hapalinae  
*Callithrix*  
 Leontocebiniae  
*Saguinus, Leontopithecus*  
 Callimiconinae  
*Callimico*  
 Hapalidae *incertae sedis*  
*Dolicebus*  
 Cebidae  
 Callicebinae  
*Callicebus*  
 Aotinae  
*Aotus*  
 Pitheciinae  
*Pithecia, Chiropotes, Cacajao, Cebupithecia*  
 Cebinae  
*Saimiri, Neosaimiri, Cebus*  
 Alouattinae  
*Alouatta, Homunculus (incl. Stirtonia, Tremacebus)*

- Atelinae  
*Lagothrix, Brachyteles, Ateles*  
 Cebidae *incertae sedis*  
*Xenothrix*

ROMER, 1966  
(a "fossil classification")

- Callitrichidae  
*Dolichocebus*  
 Cebidae  
*Cebupithecia, Homunculus, Neosaimiri, (?) Xenothrix*

## NAPIER and NAPIER, 1967

- Callitrichidae  
 Callitrichinae  
*Callithrix, Saguinus, Leontopithe...*  
 Callimiconinae  
*Callimico*  
 Cebidae  
 Aotinae  
*Aotus, Callicebus*  
 Pitheciinae  
*Pithecia, Chiropotes, Cacajao*  
 Alouattinae  
*Alouatta*  
 Cebinae  
*Cebus, Saimiri*  
 Atelinae  
*Ateles, Brachyteles, Lagothri...*

## SIMONS, 1972

- Cebidae  
 Aotinae  
*Homunculus, Aotus, Callicebus, Dolichocebus*  
 Pitheciinae  
*Cacajao, Pithecia, Chiropotes*  
 Alouattinae  
*Alouatta*  
 Cebinae  
*Cebus, Saimiri, Neosaimiri, Stirtonia*  
 Cebupitheciinae  
*Cebupithecia*  
 Atelinae  
*Ateles, Brachyteles, Lagothrix*  
 Callimiconinae  
*Callimico*  
 Callitrichidae  
*Callithrix, Saguinus, Xenothrix, Branisella*

\* For clarity, the generic names listed are the senior names, not necessarily those of the original reference. In some cases the spelling of family-group names are also emended to conform with the rules of zoological nomenclature. The listing shown for Hill, 1957-1962 is a compilation that includes his revised classification of marmosets which did not appear in his series on primate anatomy and systematics (see Hill, 1959). See Table II for additional classifications.

TABLE II

A comparison of the classification proposed here with two important classifications of recent decades

CABRERA 1958	HERSHKOVITZ 1977	ROSENBERGER (This Study)
Superfamily Platyrrhini	Infraorder Platyrrhini	Infraorder Platyrrhini
Family Cebidae	Family Callitrichidae	Family Cebidae
Subfamily Aotinae	<i>Cebuella</i>	Subfamily Cebinae
<i>Aotus</i>	<i>Callithrix</i>	Tribe Cebini
<i>Callicebus</i>	<i>Saguinus</i>	<i>Cebus</i>
Subfamily Pitheciinae	<i>Leontopithecus</i>	Tribe Saemirini
<i>Cacajao</i>	Family Callimiconidae	<i>Saimiri</i>
<i>Chiropotes</i>	<i>Callimico</i>	" <i>Saimiri</i> " ( <i>hernensis</i> )
<i>Pithecia</i>	Family Homunculidae	<i>Neosaimiri</i>
Subfamily Alouattinae	<i>Dolichocebus</i>	<i>Dolichocebus</i>
<i>Alouatta</i>	<i>Homunculus</i>	Subfamily Callitrichinae
Subfamily Cebinae	Family Cebidae	Tribe Callitrichini
<i>Cebus</i>	Subfamily Tremacebinae	<i>Callithrix</i>
	<i>Tremacebus</i>	(including <i>Cebuella</i> )
<i>Saimiri</i>		<i>Leontopithecus</i>
Subfamily Atelinae	Subfamily Sturtoniinae	<i>Saguinus</i>
<i>Ateles</i>	<i>Sturtonia</i>	Tribe Callimiconini
<i>Brachyteles</i>	Subfamily Saemirinae	<i>Callimico</i>
<i>Lagothrix</i>	<i>Neosaimiri</i>	Family Atelidae
Subfamily Callimiconinae	<i>Saimiri</i>	Subfamily Atelinae
<i>Callimico</i>	Subfamily Aotinae	Tribe Aichini
Family Callitrichidae	<i>Aotus</i>	<i>Ateles</i>
<i>Callithrix</i>	Subfamily Callicebinae	<i>Brachyteles</i>
<i>Cebuella</i>	<i>Callicebus</i>	<i>Lagothrix</i>
<i>Leontocebus</i>	Subfamily Alouattinae	Tribe Alouattini
Subgenus <i>Leontocebus</i>	<i>Alouatta</i>	<i>Alouatta</i>
Subgenus <i>Oedipomidas</i>	Subfamily Cebupitheciinae	<i>Sturtonia</i>
Subgenus <i>Marikina</i>	<i>Cebupithecia</i>	Subfamily Pitheciinae
<i>Leontideus</i>	Subfamily Pitheciinae	Tribe Pitheciini
	<i>Pithecia</i>	Subtribe Pitheciina
	<i>Chiropotes</i>	<i>Pithecia</i>
	<i>Cacajao</i>	<i>Chiropotes</i>
	Subfamily Cebinae	<i>Cacajao</i>
	<i>Cebus</i>	<i>Cebupithecia</i>
	Subfamily Atelinae	Subtribe Callicebina
	<i>Lagothrix</i>	<i>Callicebus</i>
	<i>Ateles</i>	<i>Xenothrix</i>
	<i>Brachyteles</i>	Subtribe Homunculina
	Family Xenotrichidae	<i>Homunculus</i>
	<i>Xenothrix</i>	Tribe Aotina
	Suborder <i>incertae sedis</i>	<i>Aotus</i>
	Family Bransellidae	<i>Tremacebus</i>
	<i>Bransella</i>	Family <i>incertae sedis</i>
		<i>Bransella</i>

Note that Cabrera's arrangement did not include fossils. "*Saimiri*" (*hernensis*) is included in my generic classification because I believe that it will prove to be generically distinct. *Callithrix* includes the species "*Cebuella*" *pygmaea* as well as the predominantly Brazilian forms. (See also Table I).



Even before Gray's (1821) first bifamilial classification, E. Geoffroy (1812) had identified the three major suprageneric groupings that are still considered to be basic classificatory units. Geoffroy recognized the Arctopithecii, comprised exclusively of the clawed, two-molared marmosets; the Helopithecii, including the larger species having prehensile tails, *Cebus*, *Alouatta* and the spider-woollys; and the Geopithecii, embracing the remaining platyrrhines and typified by their lack of a prehensile tail and their retention of three molar teeth. Of these assortments, the union of the marmoset genera (except for *Callimico*), has been unanimously accepted. The classificatory associations of other genera, however, have varied considerably over the years, particularly as newly accepted genera were being added to the system. Nevertheless, the development of our current classifications may be viewed as taxonomic refinement of Geoffroy's fundamental arrangement (see Fig. 1, Table I). Apart from the division of the marmosets, two other higher taxa emerged from his three groups as central foci of platyrrhine classifications, the spider-woollys ("Atelinae") and the saki-uakaris ("Pitheciinae").

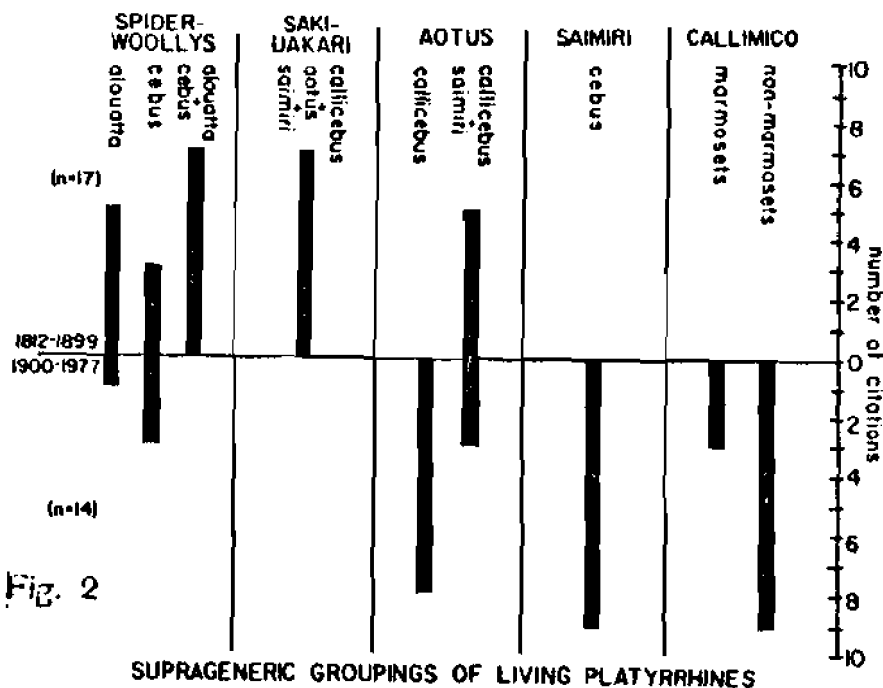


Fig. 2

Fig. 1 - The development of platyrrhine suprageneric classifications from E. Geoffroy's concepts. See text for explanation and Tables I and II for the usual generic compositions of family and subfamily groups. Double-headed horizontal arrows indicate some of the alternative placements of taxa (e.g. inclusion of *Saimiri* in the Cebinae; inclusion of *Saguinus* in the Callitricinae). *Callimico* stem is dashed because it was unknown to Geoffroy.

As with Geoffroy's approach, many systematists have relied on features of the tail for diagnosing generic groups. Some (e.g. Spix, 1823; Lesson, 1830) divided the platyrrhines as a whole into two groups, one having a prehensile tail and the other lacking it, whereas others (e.g. Gray, 1870; Dollman, 1933) employed the grasping tail as a taxonomic character at a lower level, as within families. Thus in spite of some controversy over the alliance of *Alouatta* and/or *Cebus* with the spider-woollys, both of which appeared in Geoffroy's *Helepitheci*, at least one of these genera were usually aligned with *Ateles*, *Brachyteles* and *Lagothrix* in many 19th century classifications (Fig. 2; Table 1). Until it became clear in the middle 1800's (e.g. Gray, 1849; Mivart, 1865) that the *Geopitheci* shared little in common other than the absence of features which characterized other groups, this assemblage was a standard taxonomic division (e.g. Gray, 1825; Burnett, 1828; Lesson, 1830). It has essentially been abandoned during this century as views on the affinities of *Saimiri*, *Callicebus* and *Aotus* became drastically revised (Fig. 2). In contrast, the diagnostic features of *Arctopitheci* continue to be useful, although here has been much controversy over their biological implications. In addition, there has been much debate over their use in classifying *Callimico*, which presents a mosaic of marmoset and non-marmoset morphology.

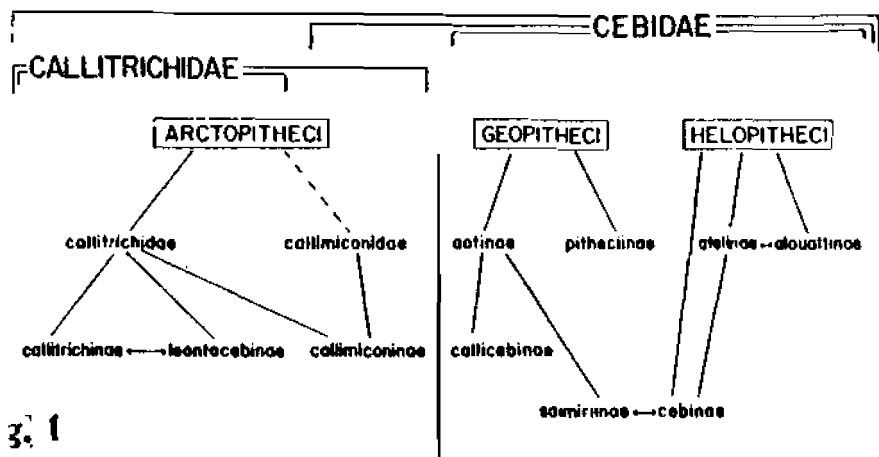


Fig. 2 - Taxonomic associations of 19th and 20th century classifications. Vertical axis presents the number of classifications in which each genus or set of genera indicated in the columns was allocated to an exclusive higher taxon containing groups or genera placed at the top row. The spider-woolly group includes *Ateles*, *Brachyteles* and *Lagothrix*; saki-uakari group includes *Pithecia*, *Chiropotes* and *Cacajao*. Note that *Callimico* was not discovered until 1904.

This breakdown of the *Geopitheci* resulted in delineation of the saki-uakari group, a comparatively stable taxonomic unit during this century defined by a fully

unique set of dental characters (e.g. Pocock, 1925; Hershkovitz, 1977; Rosenberger, 1977). It also led to the recognition of another suprageneric group of non-marmosets that is still an important conceptual focus, the Nyctipitheciinae (Mivart, 1865), although the latter's modern constituents generally differ from the original version which included *Aotus* (senior synonym of *Nyctipithecus*), *Callicebus* and *Saimiri*. However, like the heterogeneous Geopithecini, it too proved difficult to define on morphological grounds.

Subsequent modifications of this new taxon were largely the result of alternative placements of *Saimiri*. Most recent workers (e.g. Pocock, 1925; Simpson, 1945; Cabrera, 1958) were content with maintaining *Callicebus* and *Aotus* in a distinct subfamily, and placed *Saimiri* with *Cebus*. Fewer (e.g. Hill, 1960; Hershkovitz, 1977) opted to classify each of these genera in separate subfamilies. The former approach, of course, was only possible if *Cebus* was severed from the Helopithecini, a move that achieved broad acceptance only during the 20th century.

Thus, except for the much revised concept of the Geopithecini, the systematic arrangement of Geoffroy (1812) set most of the important precedents for later classifications of the platyrrhine primates. By the middle 1800's, the format of platyrrhine classification was basically similar to the arrangements that are now generally accepted (e.g. Simpson, 1945; Cabrera, 1958; Napier and Napier, 1967; Napier, 1976; Hershkovitz, 1977). The major organizational components, marmoset and non-marmosets at one level, saki-uakaris and spider-woollys at another, were fully sorted out and equally ranked as families and subfamilies. Mivart (1865), for example, employed two families of platyrrhines, with his "Cebidae" subdivided into four subfamilies (Table I). Although there has been some reshuffling of the genera between these and additional subfamilies, the framework of platyrrhine higher classification has essentially remained the same for more than a century-and-a-half.

Vestiges of Geoffroy's (1812) tripartite divisions are still apparent in discussions of platyrrhine evolution, although his direct influence on classification now seems less obvious. For example, Hershkovitz (1977) explains the adaptive radiation of the platyrrhines in terms of a series of grades of organization which correspond rather closely with the Arctopithecini, Geopithecini and Helopithecini. Together with a basic intra-platyrrhine contrast of marmoset *versus* non-marmoset grades, he also recognizes a group characterized by relatively large size and prehensile tails (*Cebus*, *Alouatta* and spider-woollys); a "marmoset-like cebid" group (*Saimiri*, *Aotus*, *Callicebus*); and a pitheciine group (*Pithecia*, *Chiropotes*, *Cacajao*). He implies that the latter is close to the marmoset-like cebids (cf. Geopithecini) and of lower grade than the prehensile-tailed forms (see 1972, Fig. 11; 1977, Fig. III.4).

## B) The Importance of *Callimico*

The discovery of *Callimico* had an important impact not only upon higher level classification but on the general interpretation of platyrrhine evolutionary history as well. *Callimico* combined in a single species the principle taxonomic characters that had been used for more than a century to distinguish the marmosets and the non-marmosets: clawed digits and three molar teeth. Since a strictly empirical definition of the marmoset and non-marmoset families could not be modified to accommodate *Callimico* and still maintain these as paired "natural" taxa, systematists were forced to reassess the basis of their classifications. Character weighting (see Simpson, 1961; Mayr, 1969), i.e., judging the phyletic significance of morphological features, became a more important part of the classification process, although most authors rarely made their interpretations explicit.

At the heart of the *Callimico* question is the controversy over whether the clawed digits and tricuspid molars of marmosets are primitive or derived features. These issues have been reviewed recently by Hershkovitz (1977) and Rosenberger (1977, 1979b). Pocock (1920, 1925; see also Gregory, 1922) cogently argued that the clawed marmosets were a rather derived branch of platyrrhines and that *Callimico*, despite its presumably more primitive molars, is best aligned with marmosets but ranked as a separate subfamily. Napier and Napier (1967), among others, have also placed *Callimico* with the marmosets but considered claws to be a primitive feature. On the other hand, Thomas (1913), Simpson (1945) and Cabrera (1958) heavily weighted the dental similarities shared by *Callimico* and the non-marmosets and assigned the genus to a subfamily of the latter. They evidently regarded marmoset claws as primitive features less indicative of phylogenetic relationships than dental features, and were perhaps willing to expand the concept of the "Cebidae", an already diverse assemblage, but unwilling to disturb the classic homogeneity of the "Callitrichidae". Simpson (1969) later concluded that the intermediate morphology of *Callimico* suggested that marmosets and non-marmosets were more closely related to one another than was implied by their placement in two families. He grouped all platyrrhines into a single family and gave *Callimico* separate subfamilial status. Dollman (1931) took the completely opposite position, placing *Callimico* in a monotypic family. This was followed by Hershkovitz (1977), who considered *Callimico* to be a very distinct lineage lacking homologous diagnostic characters of either the marmosets or the non-marmosets (see pp. 412,867). Hill (1959) himself offered two different interpretations and arrangements, first employing a unique family for the genus and later settling on subfamilial rank within his marmoset family taxon.

Taxonomically, Hill's (1959) final scheme for *Callimico* and the other marmosets also established a formal basis for a distinction that dates back to the 19th century but which had been expressed only in vernacular terms. "Marmosets", species of the genus *Callithrix*, were often separated from "tamarins", *Saguinus* and

*Leontopithecus* (and *Callimico*, according to some) on the basis of the differing crown heights of their canine and incisor teeth. Marmosets were regarded as short-tusked, with little difference between the projection of the canines and incisors, and tamarins were termed long-tusked, with strongly projecting canines and relatively low incisors. Hill allocated marmosets to the Hapalinae and tamarins to the Leontocebinæ, reserving Callimiconinae for *Callimico*.

Aside from these taxonomic debates, the *Callimico* controversy shows that some of the classifications of the 20th century were based upon a consideration of phylogenetic relationships. This contrasts with the approaches generally taken in the previous century, when zoological classifications served more as a (diagnostic) "key" (Simpson, 1961) than as an "evolutionary classification" meant to express evolutionary ideas. It was the assessment of the taxonomic distribution of morphological features among the platyrrhines, as well as the mosaically primitive and derived morphology exhibited by *Callimico*, which led many systematists to the conclusion that marmosets and non-marmosets were not so distantly related after all (e.g. Thomas, 1913; Pocock, 1925; Hill, 1959; Simpson, 1969; Rosenberger, 1979b; *contra* Hershkovitz, 1977). This view differed from the historical treatment of marmosets which often found them ranked as a separate family of platyrrhine or even as a separate Order of the primates. A similar line of phylogenetic/classificatory reasoning led first to the division of Geoffroy's Geopithecini, which appeared to be phyletically heterogeneous, then to the erection of a novel family for *Callicebus* and *Aotus*, which were thought to be relatively close relatives, and finally to the association of *Saimiri* with *Cebus*. As with the *Callimico*-marmoset affiliation, the latter grouping united species which were disparate morphologically but potentially close phylogenetically.

In summary, it appears that in the second century of platyrrhine classification, systematists such as Pocock (1925), Hill (1959), Simpson (1969) and Hershkovitz (1977) began to embrace a modernistic, evolutionary approach in developing classifications, much because of the controversy sparked by *Callimico*. However, their major concerns dealt with interesting individual genera, not with the more general question of generic and suprageneric phyletic relationship. This resulted in a finer dissection of the fundamental arrangements of Geoffroy (1812), Gray (1821, 1825) and Mivart (1965), but it did not produce a more comprehensive evaluation of the basic framework of that system. Consequently most of the currently accepted classifications of the platyrrhines (see tables I, II) employ a large number of subfamily taxa, compared with other primate groups as well as other mammalian orders of similar generic diversity. Furthermore, because so many of these equally ranked higher taxa are monospecific or represent only small groups of closely related species, there is no clear phylogenetic message embodied in any of them, in spite of Napier's (1976) comment that the recent proliferation of subfamilies "... reflects an increase in knowledge of the New World monkeys and their phylogeny" (p. 1). It appears that this organization is becoming unsatisfactory to some workers, e.g. Goodman (1975), Moynihan

(1976) and Schwartz, Tattersall and Eldredge (1978), who refrain from using any categories between the genus and the family in their classifications of platyrrhines.

### C) The Influence of the Fossil Record

Le Gros Clark stated that, "... the phylogenetic relationships of the New World monkeys can only be determined when the paleontological record becomes more completely documented" (1963:339). If so, then the basis for a comprehensive classification is severely limited since, as Rose and Fleagle (this volume) show, the fossil record of platyrrhine primates is acutely impoverished. A recent tally suggests that localities of fossil New World monkeys comprise only about 5% of the world's known nonhominid fossil primate localities (Delson, pers. comm.). The eight extinct genera comprise only 38% of the total number of platyrrhine genera recognized here, whereas fossil genera account for 60% of the classifiable catarrhine fauna (data from Szalay and Delson, 1979). But the fact that seven of eight platyrrhine genera have been named since 1950 refutes Le Gros Clark's statement, and, surely, nonpaleontological data such as amino acid sequencing and comparative anatomy are pertinent to discussion of the outlines of phylogenetic relationships.

In spite of our greater awareness of the fossil record and the tendency to employ evolutionary thinking in constructing classifications, in some respects fossils seem to have had a confounding effect upon the classification of New World monkeys. Paleontologists such as Romer (1966), Simpson (1945) and Simons (1972), as well as many of the original describers of the fossil material, have taken the usual approach and attempted to integrate these new genera with the living forms, allocating most to existing higher taxa. Hershkovitz (1977), on the other hand, erected two new platyrrhine families and three new subfamilies for these same fossils, with most of them including but one species usually represented by a single individual (see Table II). This latter system clearly represents an extreme approach, and certainly overrates the phyletic and morphologic diversity of the platyrrhines. One of the advantages of having a fossil record is that it tends to fill in the morphological and phylogenetic gaps between living species that have long since differentiated from common ancestors. In this way, much as with the case of *Callimico*, the fossil record may suggest ties between taxa that were formerly classified widely apart because of anatomical differences. *Dolichocebus* and *Iomuncubus*, for example, narrow the distance between *Cebus* and *Saimiri* and between *Aotus* and *Callicebus* respectively (see Rosenberger, 1979a, 1979b; Rose and Fleagle, this volume). The discovery of additional fossils may thus provide tests of classifications and phylogenetic hypotheses and help to expand the concepts of higher categories, many of which were initially proposed for living species alone and without much of an evolutionary basis.

### III. AN ALTERNATIVE SCHEME

As previously indicated, I have developed an alternative classification of the genera of platyrrhine primates based upon a testable hypothesis of their phylogenetic relationships as well as a scenario of their adaptive radiation. The major outlines of my inferred phylogeny, drawn specifically in terms of the classificatory issues discussed above, is presented in Fig. 3. Table II compares my classification with the arrangements of Cabrera (1958) – which does not include fossils – and Hershkovitz (1977), two influential schemes of recent decades. Apart from the fundamentally different composition of family groups, which does not divide platyrrhines into marmoset and non-marmoset units, my proposed classification differs from the conventional ones in employing additional suprageneric categories, the tribe and subtribe rankings. These levels have become extremely useful in modern rearrangements of primate higher taxa (e.g., Szalay and Delson, 1979) and were extensively used by Simpson (1945) in his classic work on mammals, although he did not apply them to the primates. This de-emphasis on family and subfamily taxa is less a reflection of my personal preference for “lumping” instead of “splitting” groups, but rather an attempt to indicate taxonomic groups that are consistent with probably phylogenetic associations.

One of the inescapable problems with this revision is that it requires that some familiar terms (esp. Cebidae, Atelinae (idae), Pitheciinae) be used in different ways. However, I believe that such a scheme allows platyrrhine classification to convey much more than conventional arrangements, which are oversplit taxonomically and also may give an erroneous impression of evolutionary relationships.

Darwin foresaw that “Our classifications will come to be, so far as they can be so made, genealogies” (1859:486). This is essentially the view of modern systematists (e.g. Simpson, 1961, Mayr, 1969), who suggest that the most *useful* classifications are those in which higher taxa are based upon phyletic affinity. I have attempted to develop such a classification by grouping genera into monophyletic groups, i.e. clusters of species sharing a unique common ancestor, although my classification is not a one-to-one correspondence with the full branching network of my phylogenetic hypothesis (Rosenberger, 1979). This principle is clearly the favored criterion for grouping genera and Simpson, among many others, argued that classifications according to grade or organization or other kinds of similarities are simply invalid if they do not conform with monophyletic relationships (1961:127). The evidence for monophyly of the various taxa, which is fully discussed elsewhere (Rosenberger, 1977, 1979a, 1979b), is their common possession of presumably “derived” rather than “primitive” characteristics. For example, the marmosets, with the exception of *Callimico*, are regarded as monophyletic because the most likely genealogical explanation for their lack of third molars (a derived feature) is that they are all the descendants of a single species which had two and not three molar teeth. In contrast, since *Callimico* has

three molars (a primitive feature), one must find other potentially derived characteristics in order to link this animal with either the marmosets or the non-marmosets. The methods and theoretical bases for this approach to phylogenetic reconstruction have been considered at length by Simpson (1961), Mayr (1969), Szalay (1977), Hecht and Edwards (1977) and others.

As I have previously implied, many of the changes encountered during the past 168 years of platyrrhine classification, especially those of this century, appear to reflect a concern for the recognition of "natural" monophyletic groups. The dissection of the Geopithecini, the removal of *Cebus* from the Helopithecini and its placement with *Saimiri*, and the controversy over *Callimico* are all examples of this. Thorington (1976) recently noted that among today's relatively uniform classifications only three subfamily groupings actually represent satisfactory (natural) groupings: marmosets (excluding *Callimico*), saki-uakaris and spider-woollys. What has not been sufficiently appreciated is the possibility that the classical concept of the non-marmoset "Cebidae" may also comprise an unnatural (polyphyletic) assemblage, i.e., including some members that are more closely related to marmosets than to other, non-marmoset genera. Indeed the monophyletic status of "Cebidae" has been tenuously questioned by several students employing various sorts of information in their studies of platyrrhine phylogeny (e.g. Dené *et al.*, 1976; Romero-Herrera *et al.*, 1976; Rosenberger, 1977). Hershkovitz has also implied this by referring to the non-marmosets as "the catch-all family Cebidae" (1974:3) and noting that "... some living subfamilies now referred to the Cebidae probably belong elsewhere" (1977:9). I know of no anatomical or biomolecular characteristics shared by the non-marmosets that are likely to be derived features suggesting that they are monophyletically related. However, there are several significant features which indicate otherwise. If this proves so, then one must question the validity and value of recognizing the non-marmosets as a family group taxon.

To briefly review the major outlines of my phylogenetic hypothesis and classification of the platyrrhines, I envision a phylogenetic dichotomy separating not the marmosets and non-marmosets from each other, but dividing the members of the Cebidae from those of the Atelidae (see Fig. 3, Table II). It appears that the cebines, *Cebus* and *Saimiri*, themselves quite closely related (e.g. Pocock, 1925; Rosenberger, 1977), and their fossil relatives (Rosenberger, 1979a) are the collateral relatives of the marmoset group. This entire assemblage of genera (termed Cebidae for reasons of priority) share in common reduced or absent third molars, enlarged canines, somewhat enlarged anterior premolars, foreshortened faces, gracile zygomatic arches and shallow, open glenoid fossae for articulation with the mandibular condyle. This combination of characters sharply contrasts with that of the atelids, as well as that of more primitive fossil and living primates (see Rose and Haegele, this volume). Additionally, the external genitalia of cebids are highly glandular, unlike those of atelids (Wislocki, 1936).



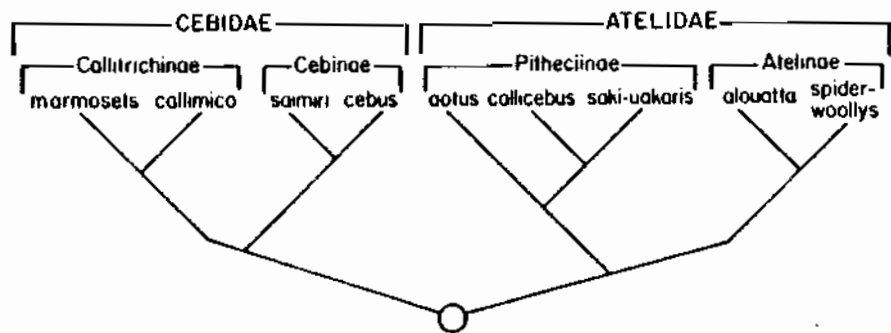


Fig. 3 - Dendrogram (cladogram) illustrating the probable phylogenetic relationships of some of the taxa discussed in the text and how these relationships are translated into a family and subfamily classification (top brackets).

This form of hypothesis, relating callitrichines to certain taxa of the known non-marmosets, has apparently been summarily dismissed by most workers. As suggested above, that bias is largely a result of the implications of classifications that were developed in pre-evolutionary times and left unchallenged. Debate on the systematic status of marmosets has focused upon argument over the primitive or derived nature of their morphology instead of the more relevant issue of their phylogenetic relationships (Szalay and Delson, 1979). A few authors (e.g. Stirton, 1951; Egozcue and Perkins, 1971) have even implied that callitrichines may be the collateral relatives of some non-marmoset genera. If additional study confirms my hypothesis of callitrichine-cebine affinities, then the interpretation that marmosets are a highly divergent lineage characterized by derived characters becomes all the more acceptable.

The callitrichines are clearly a monophyletic unit within the cebids, typified by such features as clawed digits (except for the hallux), second molar reduction, reduced hallux and pollex and a modified form of incisal occlusion. While some or all of these features are often interpreted as primitive retentions (e.g. Hershkovitz, 1977), there is a growing consensus that they are more probably derived features indicative of a divergent adaptive pattern (e.g. Rosenberger, 1977, 1979b).

Since the precise position of *Aotus trivirgatus* is not yet satisfactorily determined, the genealogical status of the Atelidae is still somewhat questionable. However, it is likely that additional study will show it to be a monophyletic group, and there appears to be no cause to separate *Aotus* (or *Tremacebus*) from the atelid group at this time. Clearly, there is no reason to genealogically align *Aotus* with any of the cebids. In contrast to the cebids, atelids present reduced buccal cingulum on the cheek teeth, relatively enlarged hypocones on upper molars, medially buttressed temporomandibular joints and a mandibular corpus whose lower border slopes distinctly ventrally, often giving the angle of the mandible an enlarged appearance.

These, too, appear to be derived features, and there are other distinguishing traits of atelids which are more primitive than the modified conditions shown by the cebids.

Within the atelids, the atelines are clearly monophyletic, as suggested by numerous unique aspects of their postcranial as well as dental morphology. The saki-uakaris have for long been accepted as a natural group, but few workers have recognized that both *Callicebus* and *Homunculus* (though the latter is not well known) also show some of the distinctive dental features of these species in a less exaggerated form. For example, all have tall, narrow lower incisors, stout canine teeth (of various heights), quite enlarged molar hypocones and cheek teeth with little crown relief.

Adaptively, if one considers the ecological, behavioral and morphological evidence together, each family may be seen as inhabiting alternative adaptive zones (Rosenberger, in press; see also Eisenberg, 1977), rather than successive grades of organization or levels of adaptive sophistication within an essentially similar milieu (e.g. Hershkovitz, 1977). The cebids, with their relatively reduced molar teeth and enhanced premolars, abbreviated faces, and keen sensory capacities, appear to be frugivore-insectivores. Their dentition suggests a functional emphasis upon the puncturing and crushing of food items with the premolar teeth rather than crushing and grinding items with the premolars and/or molars, as is common among other anthropoid primates (see Kay, 1975). Such a dietary regime is clearly the case for *Saimiri* and *Saguinus*, but the more derived, "specialized" lineages such as *Callithrix* (including *C. pygmaea*) and *Cebus* apparently developed secondary preferences and adaptations relating to gumivory (Kinzey, 1976; Coimbra-Filho and Mittermeier, 1977; Rosenberger, 1978) and a more catholic omnivorous diet (Rosenberger and Kinzey, 1976), respectively. This relates to the evolution of clawed digits and scansorial locomotion in the canopy and subcanopy by callitrichines, and the evolution of larger body size (and increased intelligence?) in *Cebus*.

The comparatively robust feeding mechanism of atelids suggests that their diet consists of more heavily masticated foods. As with cebids and nearly all anthropoids, atelids are essentially frugivorous, but unlike cebids they may also rely heavily on a non-insect protein resource. For some of the larger species, leaves may be a primary source of protein, in keeping with foraging-energetic requirements.

The relatively smaller forms, e.g. *Aotus*, *Callicebus*, *Pithecia*, *Chiropotes*, and *Cacajao*, which overlap in size with the larger cebids, appear to be less dependent on insects than the latter (e.g., Hladik, 1975). Clearly the saki-uakaris contrast strongly with *Cebus* in their foraging and dietary habits (see Mittermeier, 1977) despite their similarity in size. I suggest that heritage factors have predisposed saki-uakaris to seek foods such as seeds in place of insects, while an alternative set of heritage factors directs *Cebus* to retain its strongly insectivorous habit, despite the fact that the latter is more than twice the size of its similarly insectivorous cebid relatives.

Evidence from the fossil record (Rosenberger, 1979b) gives a few small clues as to the history of these alternative radiations, but more fossils are needed, and much more morphological and ecological and behavioral work must be done before a definitive picture of platyrrhine phylogeny and adaptive radiation can be developed and translated into a complementary classification. In the interim, I propose this classification in the hope that it will challenge all of us to reconsider the many issues that we take for granted and force us to break with pre-evolutionary concepts and guidelines.

## LITERATURE CITED

- BONAPARTE, C.L.J.L., 1831, *Saggio di una distribuzione merodica degli animale vertebrati*. Antonio Boulzaler, Rome.
- BUFFON, G.L.L., 1767, *Histoire naturelle générale et particulière avec description du cabinet du roi*. Paris, 15: 207 pp.
- BURNETT, G.T., 1828, Illustrations of the manupeda, or apes and their allies; being the arrangement of the Quadrumana or anthropomorphus beasts indicated in outline. *Quart. J. Sci. Lit. Arts*, 26: 301-307.
- CABRERA, A., 1958, Catálogo de los mamíferos de America del Sur. *Rev. Mus. Argentino Cienc. Nat. "Bernardino Rivadavia"*, 4 (1): 307 pp.
- COIMBRA-FILHO, A.F. & MITTERMEIER, R.A., 1977, Tree-gouging, exudate-eating, and the "short tusked" condition in *Callithrix* and *Cebuella*. In: D. Kleiman (ed.) *The Biology and Conservation of the Callitrichidae*. Smithsonian Institution Press, Washington, D.C., pp. 105-115.
- CRUZ LIMA, E., 1945, *Mammals of Amazonia*, vol. 1. *General Introduction and Primates*. Belém do Pará/Rio de Janeiro, 274 pp.
- DARWIN, C., 1859, *On the Origin of Species by Means of Natural Selection*. J. Murray, London, 490 pp.
- DENE, H.T., GOODMAN, M. & PRYCHODKO, W., 1976, Immunodiffusion evidence on the phylogeny of primates. In: *Molecular Anthropology*. M. Goodman, R.E. Tashian, J.H. Tashian (eds.) Plenum, New York, pp. 171-196.
- DOLLMAN, G., 1933, *Primates*, ser. 3, British Museum (Natural History) Booklet. Trustees of the British Museum, London.
- EGOZCUE, J. & PERKINS, E.M., 1967, Chromosomal evolution in the Platyrrhini. *Proc. 3rd. Int. Cong. Primat.*, 2: 131-134.
- EISENBERG, J.F., 1977, Comparative ecology and reproduction of New World monkeys. In: *The Biology and Conservation of Callitrichidae*. D. Kleiman (ed.) Smith. Inst. Press, pp. 13-22.
- ERXLEBEN, C.P., 1777, *Systema regni animalis per classes, ordines, genera, species, varietates cum synonymia at historia animalium*. Leipzig, 636 pp.
- GOODMAN, M., 1975, Protein sequence and immunological specificity: their role in phylogenetic studies of primates. In: W. P. Luckett and F.S. Szalay (eds.), *Phylogeny of the primates*. Plenum Press, N.Y., pp. 219-248.
- GRAY, J.E., 1821, On the natural arrangement of vertebrate animals. *London Med. Repost.*, 15: 296-310.
- GRAY, J.E., 1825, An outline of an attempt at the disposition of Mammalia into tribes and families, with a list of the genera apparently appertaining to each tribe. *The Ann. Phil.*, n.s., 10:337-344.
- GRAY, J.E., 1849, On some new or little known species of monkeys. *Proc. Zool. Soc. London*, 1849: 7-11.
- GRAY, J.E., 1870, *Catalogue of Monkeys, Lemurs and Fruit-eating Bats in the Collections of the British Museum*. Trustees of the British Museum, London. 137 pp.

- GREGORY, W.K., 1922, *The Origin and Evolution of the Human Dentition*. Williams and Wilkins, Baltimore, 548 pp.
- HECHT, M.K. & EDWARDS, J.L., 1977, The methodology of phylogenetic inference above the species level. In: *Major Patterns of Vertebrate Evolution*. M.K. Hecht, P.C. Goody and B.M. Hecht (eds.), Plenum Press, New York.
- HERSHKOVITZ, P., 1974, A new genus of late Oligocene monkey (Cebidae, Platyrrhini) with notes on postorbital closure and platyrrhine evolution. *Folia primat.*, 21: 1-35.
- HERSHKOVITZ, P., 1977, *Living New World Monkeys (Platyrrhini) with an Introduction to Primates*. Vol. I. University of Chicago Press, Chicago, 1117 pp.
- HILL, W.C.O., 1957, *Primates. Comparative Anatomy and Taxonomy*. Vol. III. Hapalidae. Univ. Press, Edinburgh, 354 pp.
- HILL, W.C.O., 1959, The anatomy of *Callimico goeldii* (Thomas), a primitive American primate. *Trans. Am. Phil. Soc.*, 49: 1-116.
- HILL, W.C.O., 1960, *Primates. Comparative Anatomy and Taxonomy*. Vol. IV. Cebidae. Part A. University Press, Edinburgh, 523 pp.
- HILL, W.C.O., 1962, *Primates. Comparative Anatomy and Taxonomy*. Vol. V. Cebidae, Part B. Univ. Press, Edinburgh, 537 pp.
- HLADIK, C.M., 1975, Ecology, diet and social patterning in Old and New World primates. In: *Socioecology and Psychology of Primates*. R.H. Tuttle, (ed.), World Anthropology, Mouton, The Hague, pp. 3-35.
- KAY, R.F., 1975, The functional adaptations of primate molar teeth. *Am. J. Phys. Anthropol.*, 43: 195-216.
- KINZEY, W.G., ROSENBERGER, A.L. & RAMIREZ, M., 1975, Vertical clinging and leaping in a neo-tropical anthropoid. *Nature*, 255: 327-328.
- LeGROS CLARK, W.E., 1963, *The Antecedents of Man*. Harper Torchbook (ed.) Harper and Row, New York, 374 pp.
- LESSON, R.P., 1830, Compléments des œuvres de Buffon, vol. 4. P. Frères and Roret, Paris.
- LINNAEUS, C., 1758, *Systema Naturae*. Stockholm, Laurentii Salvii, 823 pp.
- MAYR, E., 1969, *Principles of Systematic Zoology*. McGraw-Hill Publ. Co., New York, 428 pp.
- MILLER, G.S., Jr., 1924, List of North American recent mammals. *Bull. U.S. Nat. Mus.*, 128: 167-172.
- MITTERMEIER, R.A., 1977, *Distribution, Synecology and Conservation of Surinam Monkeys*. Unpublished dissertation, Harvard University, Cambridge.
- MIVART, S.G., 1865, Contributions towards a more complete knowledge of the axial skeleton in the primates. *Proc. Zool. Soc.*, London 1865: 542-592.
- MOYNIHAN, M., 1975, *The New World Monkeys*. Princeton Univ. Press, Princeton, 262 pp.
- NAPIER, P.H., 1976, *Catalogue of Primates in the British Museum (Natural History)*. Part 1: Families Callitrichidae and Cebidae. British Museum (Natural History), 121 pp.
- NAPIER, J. R. & NAPIER, P.H., 1967, *A Handbook of Living Primates*. Academic Press, New York, 456 pp.
- POCOCK, R.I., 1920, On the external characters of the South American monkeys. *Proc. Zool. Soc. London*, 1920: 91-113.
- POCOCK, R.I., 1925, Additional notes on the external characters of some platyrrhine monkeys. *Proc. Zool. Soc. London*, 1925: 27-47.
- ROMER, A.S., 1966, *Vertebrate Paleontology*. 3rd ed. Univ. Chicago Press, Chicago, 468 pp.
- ROMERO-HERRERA, A.E., LEHMAN, H., LOYSEY, K.A. & FRIDAY, A.E., 1976, Evolution of myoglobin amino-acid sequences in primates and other vertebrates. In: *Molecular Anthropology*. M. Goodman, R.E. Tashian and J.H. Tashian (eds.), Academic Press, N.Y., pp. 289-300.
- ROSE, K.D. & FLEAGLE, J.G., 1980, The fossil history of nonhuman primates in the Americas.
- ROSENBERGER, A.L., 1977, *Xenothrix* and ceboid phylogeny. *J. Hum. Evol.*, 6: 461-481.
- ROSENBERGER, A.L., 1978, Loss of incisor enamel in marmosets. *J. Mammal.* 59: 207-208.
- ROSENBERGER, A.L., 1979a, Cranial anatomy and implications of *Dolichocebus*, a late Oligocene ceboid primate. *Nature*, 279: 416-418.
- ROSENBERGER, A.L., 1979b, *Phylogeny, evolution and classification of New World monkeys (Platyrrhini, Primates)*. Unpublished dissertation, C.U.N.Y., New York.

- ROSENBERGER, A.L., Gradistic views and adaptive radiation of the platyrrhine primates. In press.
- ROSENBERGER, A.L. & KINZEY, W.G., 1976, Functional patterns of molar occlusion in platyrrhine primates. *Am. J. Phys. Anthropol.*, 45: 281-298.
- SCHWARTZ, J., TATTERSALL, I. & ELDREDGE, N., 1978, Phylogeny and classification of the primates revisited. *Yrbk. Phys. Anthro.*, 21: 95-133.
- SIMONS, E.L., 1972, *Primate evolution: an introduction to man's place in nature*. Macmillan, New York, 322 pp.
- SIMPSON, G.G., 1945, The principles of classification and classification of mammals. *Bull. Amer. Mus. Nat. Hist.*, 85: 1-350.
- SIMPSON, G.G., 1961, *Principles of Animal Taxonomy*. Columbia Univ. Press, 247 pp.
- SIMPSON, G.G., 1969, South American mammals. In: *Biogeography and Ecology*. E.J. Fittkau, J. Illies, H. Klinge, G.H. Schwabe and H. Siolo (eds.). Mouton, The Hague, pp. 879-909.
- SPIX, J., 1823, *Simiarum et Vespertillarum Brasiliensis Species Novae*. Monaco, 72 pp.
- STIRTON, R.A., 1951, Ceboid monkeys from the miocene of Columbia. *Univ. Calif. Publ. Bull. Acad. Sci.*, 28: 315-356.
- SZALAY, F.S., 1977, Ancestors, descendants, sister groups and testing of phylogenetic hypothesis. *Syst. Zool.*, 26: 12-18.
- SZALAY, F.S. & DELSON, E., 1979, *Evolutionary History of Primates*. Academic Press, New York.
- THOMAS, O., 1903, Notes on South American monkeys, bats, carnivores, and rodents, with descriptions of new species. *Ann. Mag. Nat. Hist.*, ser. 7, 12: 455-464.
- THOMAS, O., 1913, On some rare Amazonian mammals from the collection of the Pars Museum. *Ann. Mag. Nat. Hist.*, ser. 8, 11: 130-136.
- THORINGTON, R.W. Jr., 1976, The systematics of New World monkeys. In: *Firs. International Conference on Conservation and Utilization of American Nonhuman Primates in Biomedical Research*. PAHO Scient. Publ. No. 347, Washington, D.C., pp. 8-18.
- WISLOCKI, G.B., 1936, The external genitalia of the simian primates. *Human Biol.*, 8: 309-347.