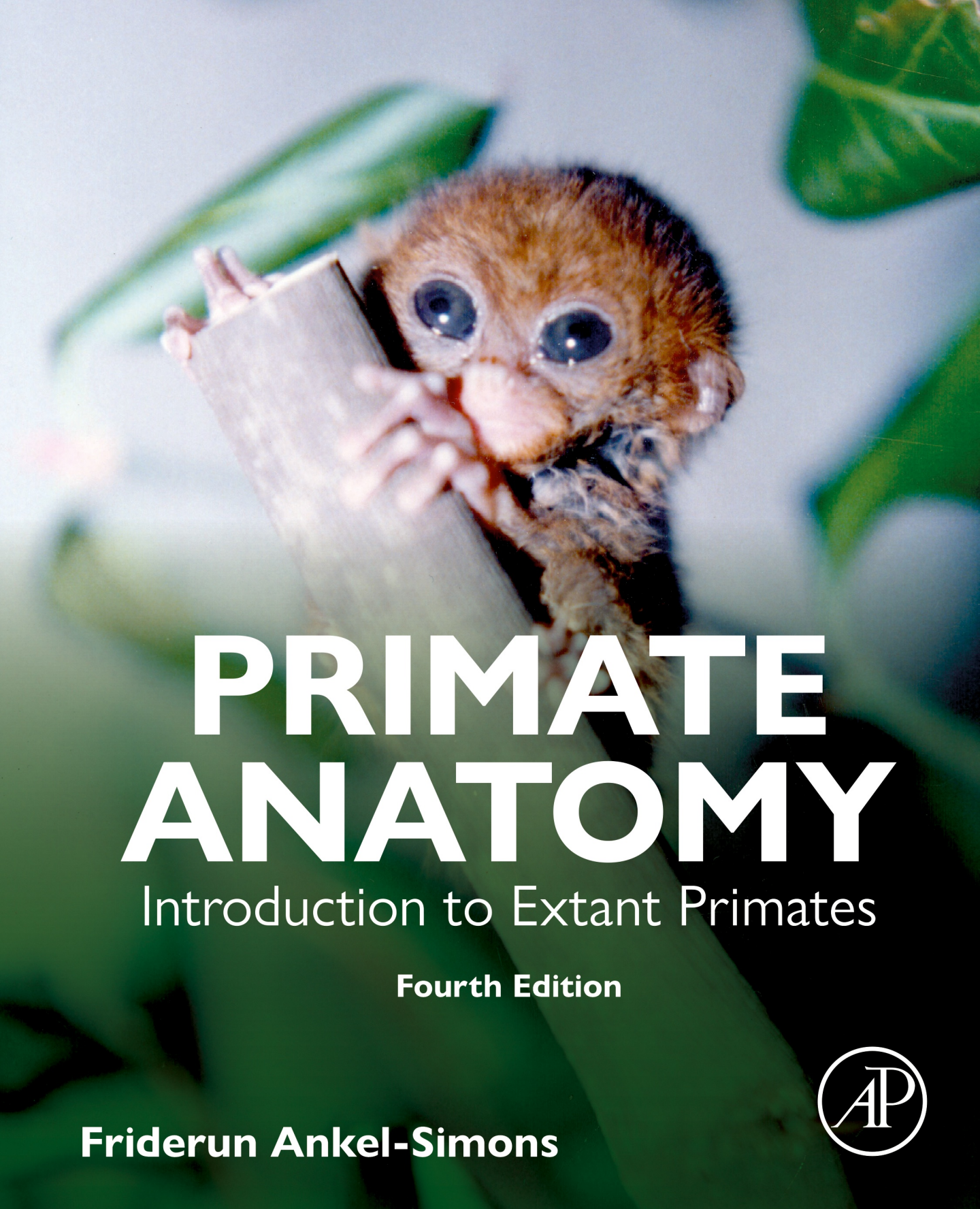

# PRIMATE ANATOMY

## Introduction to Extant Primates

**Fourth Edition**

**Friderun Ankel-Simons**

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## Introduction to Extant Primates

## FOURTH EDITION

FRIDERUN ANKEL-SIMONS
*Duke University, Durham, NC, United States*

ELSEVIER

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# Contents

# Preface

It all began in the 1960s and 1970s while I was teaching at the Anthropological Institute and Museum of the University of Zürich, Switzerland, for 7 years, trying to answer all too many unanswered questions that were raised by our inquisitive students. This resulted in the publication of Friderun Ankel, "Einführung in die Primatenkunde" (Ankel, 1970).

More than 50 years later, in a totally changed and different world, the 4th edition of *Primate Anatomy* is issued. The basic anatomy of the mammal order "Primates" has not changed, but the scary new world of genetics has morphed indeed. Recently created molecular technologies such as CRISPR (clustered regularly interspaced short palindromic repeat) have opened the door—or Pandora's Box—to gene editing with all the positive and negative consequences (Ledford, 2022; Eisenstein, 2022; Doudna and Steinberg, 2017; Lander, 2016). When scientific endeavor crosses invisible barriers of ethics creating the option of gene editing, we arrive at the edge of science and the limits of primate anatomy.

We are trying to understand and even explain the vast chasm between the viewpoints and insights voiced in discussions focusing on human overpopulation on planet Earth by various professions. The drastically contrasting opinions voiced by prominent economists, social scientists, environmental activists, and agriculturalists are in stark contrast, saying "it does not matter" compared to the perception voiced by biologists. This situation is apparent at the same time with the apparently unstoppable tidal wave of human overpopulation and with worldwide climate change and pandemics. There are now crucial reasons to perceive planet Earth with a changed outlook. Therefore, I decided to conserve the facts in the new edition that remain unchanged since the 2007 third edition of *Primate Anatomy*. Morphology and anatomical characteristics do not change over short periods of time, like years, decades, centuries, or even millenniums. It can take many more than thousands of years to reshape morphological and physiological adaptations. Thus, I am pointing out new insights and outlooks where needed, hoping to accept our own primate nature and the daunting future for our wonderful, unique, and mesmerizing planet Earth—our one and only home base.

My heartfelt thanks go to my colleagues Linda Taylor, Jeffrey Laitman, and T.D. Smith for their support and encouragement. Simonetta Harrison, Ron Meris, Palak Gupta, and Fahmida Sultana helped me greatly with mastering multiple logical problems while editing the third edition of *Primate Anatomy*. Also thanks to Sugandhi Govindarajalu, Project manager at Straive. Any mistakes are mine, as it is my book.

*Friderun Ankel-Simons*

Peoria, Arizona, August 2023

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CHAPTER

# 1

# New developments—Nonhuman primates in peril

OUTLINE



The order Primates is one of the most diversified groups of living mammals, ranging from lemurs to humans. Members of this order have always been the focus of human curiosity, and many primates are astonishingly similar, both behaviorally and anatomically, to human beings, the most successful and progressive species of the order, *Homo sapiens*. Sadly, humans have become the only extant primate species to have become an invasive species worldwide.

It is helpful to look over the list of taxonomic names to become familiar with the wide variety and diversity of primates (Chapter 4). Each species description will enable the reader to more readily understand the subsequent chapters. Naturally, it needs patience to become familiar with all of the primate groups, and this knowledge will improve gradually with time. One should become acquainted with these groups, but there is no need to memorize the list of names. These names will fall into place with increased knowledge of and interest in the primates and their characteristics.

It must be kept in mind, however, that taxonomic assignments are subject to constant change, new discovery, and discussion. The following list is the foundation and a necessary frame of reference for informed discussion about primates. New discoveries can either change the taxonomic placement of known animals through new insights or add newly discovered species that were hitherto unknown to science. The astonishing increase of species in many genera can be credited to two factors: the increase in the number of primatologists in the field worldwide who find hitherto unknown taxa and the proliferation of new assignments by primatologists who stay home and increase and change the number of species by desktop contemplations.


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## New developments

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Patricia Wright and Elwyn Simons have been working in Madagascar since 1981, actively promoting the conservation of rare and endangered lemurs for the future. Both were crucially involved in opening up the magic island for international research and were soon followed by a myriad of others. Because of this, there is no doubt that our knowledge about Malagasy lemurs in particular and Madagascar's natural history in general has been vastly increased.

The following lineup of living primates is based on the taxonomy of Simons (1972), which was brought up to the knowledge in 1999 with the help of Patricia Wright and

Elwyn Simons for prosimians, Thomas Struhsaker for colobines, and Leslie Digby for callitrichids. The list has been amended for this edition using the texts by Groves (2001) and Geissmann (2003) for all primates, Grubb et al. (2003) for African primates, Brandon-Jones et al. (2004) for Asian primates, and Wright et al. (2003) for genus *Tarsius.* Unlike Grubb et al. (2003), we are not dealing with subspecies in our lineup of living primates. The taxonomy and phylogeny of the subtribe Papionina has long been under discussion ( Jolly, 2003). It appears that the puzzle surrounding the baboons has now been solved to some extent by a very interesting and thorough evaluation of cranial allometry, phylogeny, geographic distribution, and systematics of the papionins. The information has been evaluated with the help of geometric morphometric analysis landmark data and resulted in the confirmation of three genera: *Mandrillus* with two species, *Theropithecus* with one species, and *Papio* with one species, *P. hamadryas,* which has six subspecies (Frost et al., 2003). We are not listing subspecies because the taxonomic list of all primates would be too long and cumbersome for this chapter. Also, the postcranial morphology and dentition of the papionins have been evaluated to reassess molecular evidence that had separated terrestrial mangabeys (genus *Cercocebus*) together with genus *Mandrillus* from the arboreal mangabeys (genus *Lophocebus*) together with genus *Papio.* Fleagle and McGraw (2002) have established that postcranial and dental characters support a previous molecular assignment.

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The book, dealing with all extant primates (Rowe, 1996), provides detailed information about each species and is illustrated by excellent photographs. These various resources have all helped to complete the following taxonomic lineup of living primates. Their geographic distribution is shown in Figure 1.1.

Many subspecies of Malagasy lemurs and other primates have been elevated to species level (Rasolooarison et al., 2000; Groves, 2001; Brandon-Jones et al., 2004; Thalmann and Geissmann, 2000; Thalmann and Geissman, 2005). The "new" species are included in the lineup, although the justification for such changes in taxonomic ranking remains under discussion. New and formerly unfamiliar names are used in publications, and therefore they are listed here.

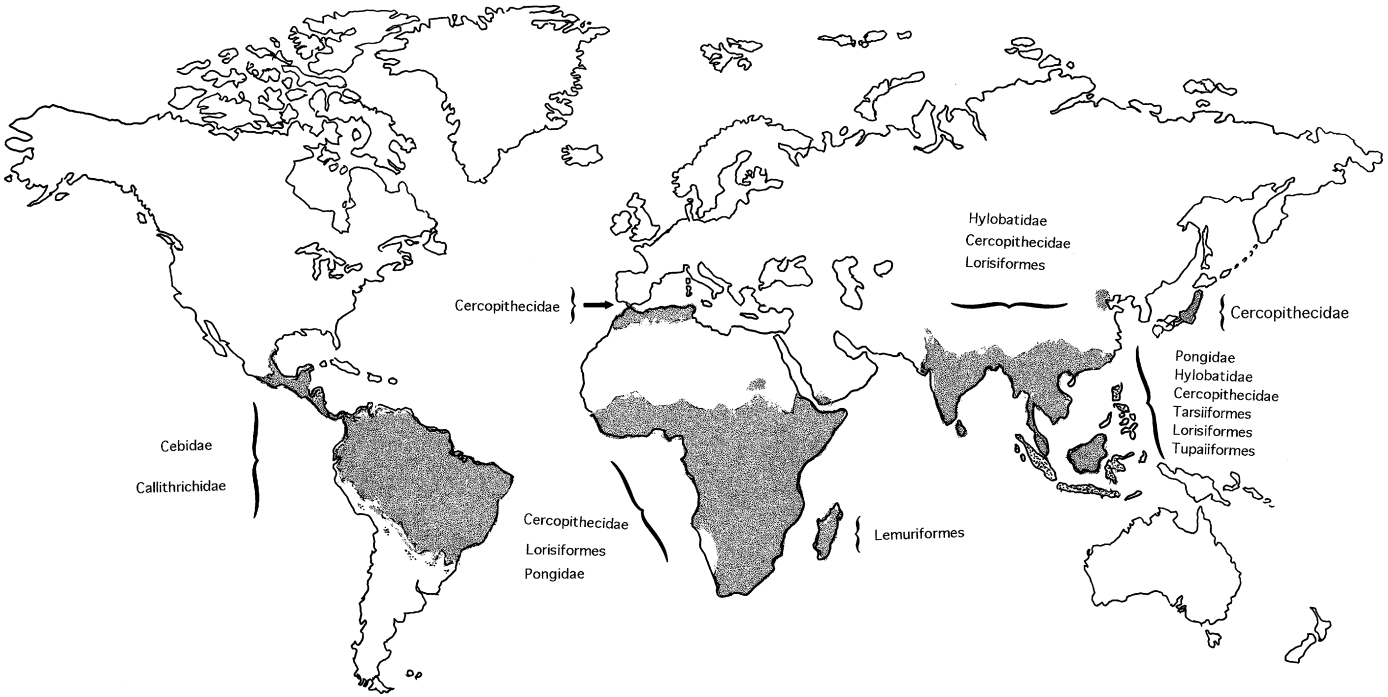


**FIGURE 1.1** Worldwide distribution of primates: not unlike body weight data, animal distribution maps are subject to constant change resulting from human impact, newly confirmed sightings, and other unpredictable factors.

CHAPTER

# 2

# Taxonomy

OUTLINE



Taxonomy often is a jumble of observable facts, individual judgment, failure to precisely identify the species involved in genetic research (Rylands, 2007), and misleading variable parameters. It can be based on rather flexible personal observations, sundry data, speculation, and various increasingly elaborate technologies. Taxonomy is ever-changing and not carved in stone. Therefore, we will maintain the basic, well-established, and traditional genus and species assignments to avoid confusion. Taxonomy should be the reliable foundation for understanding which living organism is discussed. Unfortunately, there can be confusion and misunderstanding involved. However, the recent expansive accumulation of newly described and named genera and species that are based on genetical data often involve morphologically very similar organisms, e.g., the newly described genera and species of prosimians such as *Cheirogaleus*, *Microcebus*, or *Loris* and even the enigmatic genus *Tarsius*. Obviously, all are small-bodied primates. To always find up-to-date information about newly discovered and named new or renamed previously named nonhuman primates, see Mittermeier IUCN/SCS Primate Specialist Group, a reliable source of information that is regularly updated. These "new" genera and species are based on genetic findings.

Following here are a few interesting, even surprising, examples of recent taxonomic ventures.

Genus ***Cheirogaleus*** Previously accepted were two species that have subsequently been increased to seven *Cheirogaleus* species (Groves, 2000). Now there are at least seven more genetically differentiated *Cheirogaleus* species that are difficult, if not impossible, to identify using morphological features (Lei et al., 2015).

**Genus *Microcebus***

The number of newly described *Microcebus* species continues to increase. Originally, there were but two species: *M. murinus* with gray fur and *M. rufus,* having reddish to brown fur (Rasolooarison et al., 2000). In 2016, there were twenty-four DNA species that, however, also are morphologically very similar (Olivieri et al., 2007; Schüßler et al., 2023).

Genus ***Nycticebus***

There is a newly described Slow Loris species *Nycticebus kayan*, and the Pygmy Slow Loris got a new genus name: *Xanthonycticebus pygmaeus* (Nekaris and Nijman, 2022), both because of morphological and genetic differences from *Nycticebus.*

Genus ***Tarsius***

There have been two new genera added and changed from the genus *Tarsius*: *Cephalopachus bancanus bancanus* (Syafutra et al., 2019) and *Carlito syrichta syrichta* (Groves and Shekelle, 2010). And there are now 14 new species. In 2017, two other species were added to the genus *Tarsius*: *T. spectrumgurskyae* and *T. supriatnai.* (Shekelle et al., 2017). Adding to the "*Tarsius* mystery," Hofer (1979) said this about the classification of Tarsiers as "Haplorrhini": "A gross anatomical and microscopical study of the external nose of *Tarsius bancanus borneanus* demonstrated the typical strepsirrhine shape of the nostrils and an extreme platyrrhine condition. The wide internarial area possesses no sinus hairs. The concept of strepsirrhinism and haplorrhinism may be used to characterize the different shapes of the nostrils but they do not have any taxonomical significance."

**And another, enigmatic order of Mammals: Dermoptera or Colugos has moved into closer taxonomic relationship with Primates**

Family Cynocephalidae is *with two genera and species, Galeopterus variegates* and *Cynocephalus volans.* And only as recently as 2007 has the Mammal order Dermoptera: Colugos, family Cynocephalidae, been assigned a close taxonomic relationship with primates (Janečka et al., 2007). There are just two living species of colugos: the Sunda "flying lemur" *Galeopterus variegatus* and the Philippine "flying lemur" *Cynocephalus volans*, and they glided into a closer relationship with Primates than Tupaidae. Never mind that colugos are neither Lemurs nor do they actively fly as they swiftly glide downward. Basically, they are shaped like small, overall furry Frisbees: their body a patagium with nothing but the short neck and head as well as four short extremities sticking out.

***Tupaia***

Recently, there were 19 species in the genus *Tupaia.* But now, a new species was described in 2020: *Tupaia danghuyhuynhi,* spec. nov., and thus, there are 20.

In 2015, Tupaiidae was classified into five different genera. Four of these (*Anathana* [*A. ellioti*], *Dendrogale* [*D. murina* and *D. melanura*], *Urogale* [*U. everetti*], and *Tupaia*) are combined together within the taxonomical family, Tupaiidae. There is just one species in the family Ptilocercinae: *Ptilocercus lowii*.

**Genera *Simias* and *Allenopithecus***

During a recent survey of collections at the Finnish Museum of Natural History (FMNH), two dilapidated and incorrectly assigned Primate specimens were discovered and newly identified (Pihlstrom and Lankinen, 2018; Whittaker et al., 2006)

**Genera *Simias* and *Nasalis***

Another intriguing taxonomy puzzle. Could *Simias concolor* and *Nasalis concolor* be the same? If nothing else, they share the same geographical region and the same common name: Simaboku monkey (Whittaker et al., 2006).

## New developments

As discussed in Chapter 1, the order Primates is one of the most diversified groups of living mammals, ranging from lemurs to humans. Members of the order have always been the focus of human curiosity, and many primates are astonishingly similar, both behaviorally and anatomically, to human beings, the most successful and progressive species of the order: *Homo sapiens.*

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CHAPTER

# 3

# A history and objectives of primatology

OUTLINE



## The state of affairs

The science of primatology is concerned with the study of those mammals that are most closely related to human beings. Humans, being the most successful and erudite of all mammals, have been fascinated by the challenge of discovering their own place in the complicated realm of nature ever since they began to reason. Our closest mammal relatives constitute the order Primates, which includes four main living groups: prosimians, monkeys of the Old and New Worlds, greater and lesser apes, and humans. Some more distantly related forms such as the tree shrews, colugos, elephant shrews, and opossums may belong in separate mammal orders but are also of comparative interest. Today primatology has blossomed into an important subdiscipline of biology and has developed different focal points such as the study of primate morphology, history, and function as well as primate social behavior and molecular primatology.

Primatology as a distinctive field within biology did not exist until the second half of the 1950s. Despite the fact that magnificent monographs such as those of Owens and Peters on the aye aye had been published in the middle of the ninetieth century, knowledge about primates in general was sparse before the twentieth century.

Even though humans have always been spellbound by their close relatives, the monkeys and the apes, these were regarded for a long time as curiosities rather than our kin, and that learning about them would help us to better understand ourselves. Primates dressed in human attire, such as the organ churning, highly intelligent South American monkey, the capuchin, have played a great part in our history as subjects of amusement and even as pets.


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The thought processes leading to the development of primatology took root when Darwin's theory of evolution by natural selection was first applied by Thomas Henry Huxley (1825–95) to interpret the comparative biology of humans and apes. In his 1863 essay, "Man's Place in Nature," Huxley first dealt with many of the topics that have remained important in primatology up to the present day. Such topics include the position of human beings among the other primates and the question of our descent from animals that were of simpler and different grades of organization. He stated without hesitation that human beings had evolved from other animals. Huxley was also one of the first to show in great detail that humans were most closely related to the African apes.

For those who engage in research on the primates, primatology has never seemed more relevant than at present. Arising from diverse beginnings, its subdisciplines are becoming more closely integrated. As many more precise evaluations and data about primates are published, the subject is making increasing contributions to biological studies. With the added recognition of problems related to endeavors of conservation of extant primate species, rapidly encroaching human overpopulation, and the fast expanding demands on the world's environments and natural resources by the multitude of human beings, primatology has become a cutting-edge scientific discipline that provides an information base for strategies that are aimed to protect our planet from environmental disasters. Religious disagreements, human hatred, hunger and preemptive wars are turning this planet into a world of vanishing hope for all primates.

Within the biological sciences, primatology is closest to physical—or biological—anthropology and human biology, disciplines that are specifically concerned with analysis of our own species, *Homo sapiens*—the only species capable of seeking a certain degree of self-understanding.

Despite centuries of developing human self-interest, many aspects of human biology and primatology have only recently been explored. As disciplines concerned mainly with one species, *H. sapiens,* anthropology and cognition have a unique coincidence of subject and object, but most physical anthropologists also study nonhuman primates as analogs to ourselves. Humans are still fascinated by their near relatives; we continue to be amused, even shocked, by the many parallels between primates and ourselves. There is one big difference between humans and all the other primates: only humans have religion, with all the disturbing consequences it can cause.

## History

One could compile a lengthy account of references to primates in literature, but here a brief outline must suffice. In the fourth century B.C., the philosopher Aristotle (384–322 B.C.), in his *Historia animalium,* initially divided monkeys into three main groups: 1) the *pithekoi,* forms with reduced tails; 2) the *keboi,* forms with long tails; and 3) the *kynokephaloi,* dog-headed forms, namely, the baboons. Pliny the Elder (circa 23–79 A.D.), in his *Natural History,* observed that the primates are much like humans. Later, Galen of Pergamon (c. 130–200) dissected both monkeys and apes and pointed out that they closely resembled humans in their bony skeletons and in their intestinal, muscular, nervous, and vascular systems. He wisely admonished his students to study the primates to gain a better understanding of human anatomy.

Marco Polo (?1254–?1324), who traveled widely in the Orient in the thirteenth century, described strange, small, humanlike creatures. This was perhaps the first reference to gibbons. From Marco Polo's time on, scholars in Europe showed an increasing interest in the natural world. By the sixteenth century, Konrad von Gesner (1516–65) in Switzerland reviewed all he could find about primates for his *Natural History.* This outstanding early work reflects, together with a certain credulousness and the superstition characteristic of those times, the inception of ecstatic feelings about the wonders of the natural world. In 1699, an English scholar, Edward Tyson, published the first study of the anatomy of an ape, basing his work on the body of a "pygmy" from Angola that was later understood to be that of a young chimpanzee. Despite its early date, this study was remarkably accurate. In the 300 years after this study, many descriptions of monkeys and apes were published in Europe. Their authors included the well-known natural historians Johann Friedrich Blumenbach, Georges Buffon, Georges Cuvier, Johann Christian Polycarp Erxleben, Johann Karl Wilhelm Illiger, Richard Owen, Thomas Pennant, and Étienne Geoffrey Saint-Hilaire, all of whom added significantly to knowledge of primates.

Attempts to organize the taxonomy of primates began in Sweden in 1758 when the naturalist Linnaeus published a remarkable work. This was the tenth edition of his famous book, *Systema Naturae,* in which he named one of the orders of mammals Primates. In this order, he placed, together with humans, a genus of ape, of monkey, of lemur, and of bat. Twenty-three years before this publication, in the first edition of *Systema Naturae,* he had already grouped humans, apes, and monkeys together, as well as (with unintentional humor) the sloths. These he had ranked together in one group, the "anthropomorphic" or humanlike creatures. Amazingly, it turns out that several of the large, subfossil lemurs from Madagascar have been called "sloth lemurs" because of their astonishing morphological similarity with sloths (E.L. Simons et al., 1992; Jungers et al., 1997). For his objective, Linnaeus systematically ranked animals only according to their obvious, overall similarities and drew no conclusions about a place in nature for humans. Nevertheless, his bold step in uniting humans with animals caused much protest, and others soon began to reassert the uniqueness of humans by separating them as distantly as possible from all other living organisms.

Thus, Johann Friedrich Blumenbach, in 1719, separated humans from an embarrassingly close relationship to apes by creating two orders. One was the order Bimana (meaning two handed) for humans and a second the order Quadrumana (meaning four handed) for all remaining primates. The same distinction was made by Baron Cuvier nine years later, and the use of these two terms persisted for nearly 100 years thereafter. Differing with this usage, Illiger (1811) took as the central concept of his systematics the uprightness of humans and established for them the order Erecta. Owen (1863) believed that the difference between humans and the other primates was great enough to create a much higher category in the animal kingdom for humankind. He coined for humans the subclass Archencephala, those with the most advanced kind of brains.

Beginning in 1859, Darwin brought a fresh point of view to the discussion of our relationship to other animals. For him, the similarities between different kinds of organisms were due neither to design nor to chance. He recognized that the relationships of living things to each other showed that the similarities among animals are due to common descent. Darwin thereby made a critical push toward a new kind of biological thinking, although he avoided, at that time, the implications of natural selection as the basis for the origin of *Homo sapiens.*

A few years later Thomas Henry Huxley (1863) took his significant step of showing the close relationship between humans and African apes in his article "*Man's Place in Nature*." Finally, Charles Darwin (1861/1871) himself, in *The Descent of Man*, made an elaborate study comparing human and animal. From then on, many scientists throughout the last decades of the nineteenth century and during the early part of the twentieth century dealt with the close ties between humans and the other primates as the full impact of the biological nature of humans became evident. Together, these publications have shown that primatology provides a necessary background for understanding the main stages of human evolution.

Because of the identity of subject and object, a high level of subjectivity characterizes much that has been done in anthropology, and this has been intruded into the study of our species. Primatology as a whole provides new and better sources of more objective information that should help to clarify some of the phases of understanding human evolution that have been controversial in the past. Consequently, it is hoped that *H. sapiens* may be dealt with more objectively if it is recognized as merely one species of the order Primates.

## Primatology as a branch of biology

Biology is essentially a comparative science. The relationships of organisms to one to another, their similarities and their distinctions, are the bases of contrast. In and of itself, a single biological object has no context. Because it is impossible to avoid recognizing the many similarities between humans and apes, the study of humans as not different from primates gains both strength and objectivity in a comparative approach. Were it not for the uniqueness of humans in the natural world, there would be less importance to primatology; there would be no more interest in this particular mammalian order than in the others. Some other orders are more diverse than Primates—Rodentia, Chiroptera, Artiodactyla—and each mammalian order has evolved its own distinctive specializations, such as the flight of bats. As many of the strengths of present-day physical anthropology are derived from primatology, primatology in turn is dependent on understanding other animals, especially other nonprimate mammals. Thus, primatology cannot be taken as an entirely self-contained field.

In considering more recent advances in primatology, one thinks automatically of such leading scientists in the field as the English anatomist Sir Wilfrid Le Gros Clark or of Adolph Hans Schultz of Zürich, both of whom, from early in the twentieth century, began publishing a series of fundamental contributions to primatology.[1]

Wilfrid Edward Le Gros Clark (1896–1971) was a young physician and officer in the English army when he was sent to Borneo. There, in his spare time, he focused his interest on the study of human biology, primates in general and tree shrews, as well as tarsiers in particular. His keen curiosity and knowledge laid the foundation for a prominent career in anatomy and primatology after his return to Great Britain. He published detailed studies about the tree shrews and was appointed professor of anatomy at Oxford University in 1934. His

[1] A book about A.H. Schultz that was published in 2004 by Chaoui fails on two levels. The author sadly misrepresents the complex personality of a scholar who arguably was the most preeminent primatologist of his time. Also, Chaoui unfortunately mangles the intricate complexities of the German language.

thoughts and books about human and primate evolution became the leading texts for generations of biological anthropologists and still have great applicability to the formulation of theories of primate and human evolution. These influential books are as follows: *Early Forerunners of Man* (1934), *History of the Primates* (1949), *Antecedents of Man* (1959), and *Man-apes or Ape-men?* (1967). He was also one of the leading scientists who discovered and exposed the "Piltdown Man" forgery.[2]

Five years older than Le Gros Clark, the young Swiss anthropologist Adolph Hans Schultz (1891–1976) went to the New World in 1925, where he was appointed professor of anatomy at Johns Hopkins University in Baltimore. During his tenure there (1925–51) he launched many expeditions to far-flung corners of the world to study and collect living primates. Schultz assembled an impressive collection of primate skulls and skeletons, as well as primate fetuses. He was especially intrigued by the variability of living primates and published many scientific reports that document primate morphology in comparison with the anatomy of modern humans. In 1951, Schultz returned to Zürich, Switzerland, to take over the directorship of the Institute of Anthropology at the university there. He brought a sizable collection of primate skeletons and soft tissues that he had collected while at Johns Hopkins with his own personal funding. Schultz established one of the most extensive primate collections at the institute in Zürich and added to this collection during his lifetime. He published a host of scientific papers about extant primates that are still fundamental resources of information about measurements and details of primate morphology for today's students.

Early on it was believed that individual monkeys within a species were very much alike, if not identical, to each other. Thus, it was not considered incorrect to generalize from findings based on one or two individual monkeys to the whole species. Now we know that the high degree of present human structural and behavioral variability extends not only to other primate species but to nonprimates as well. This fact was initially documented thoroughly and extensively by the father of primatology, Adolph Hans Schultz. The significance of variability in morphological studies was taught at Johns Hopkins under Schultz's tutelage and in Zürich to the extent that young students of zoology who took his courses in primatology tended to protest against the focus on variability. These students were still being taught in other classes that all animals belonging to one species were morphologically identical to each other, which appeared to be a much simpler concept. We now know that organismal individuality is also expressed in the uniqueness of every creature's DNA. Today this fact is widely applied in forensic investigations.

It is clear that because of the high individual variability of primates, we have a rich source of possible error in the interpretation of fossil primates. By understanding the range of variation found within and between species of related living primates, we can avoid this error. This knowledge of variability has become a principal basis for the latest taxonomic revisions of fossil finds. In general, such revisions suggest grouping of fossils that previously had separate names, and this in turn makes the picture of primate evolutionary history easier to grasp.

[2]In 1912, a sensational announcement proclaimed that a Paleolithic human skull and mandible had been discovered in a fossil-bearing quarry near Piltdown, England (Dawson and Smith Woodward, 1912). This find immediately caused much controversy, and 40 years later was revealed to be a hoax by John S. Weiner, Kenneth P. Oakley, and Wilfrid E. Le Gros Clark (1953; Weiner, Introduction and Afterword by Springer, 2003).

In retrospect it becomes evident that the term "primatology" seems to have been first used in print as recently as 1941 by T.C. Ruch. Even though a comprehensive focus on primates is a comparatively recent scientific development, the literature in this field has been expanding rapidly since the late 1950s. Now, more than 40 years have passed since the introduction of *Folia Primatologica,* the first regularly published journal reporting research on primates, and it is still going strong. In the meantime, numerous other scientific magazines such as the *International Journal of Primatology* and the *American Journal of Primatology* have joined the primatologists' printed forum. Universities all over the world have initiated educational programs in primatology, and numerous students focus their life goal on the study of primates. In 1968, the International Society of Primatology had its first meeting at the University of Gießen in Germany and was soon followed by other national and international societies of primatology.

The recognition that humans are unique in many ways but at the same time nothing but a mammal biologically is as ancient as Linnaeus's (1758) decision to classify humans among primates. This biological character of our animal nature has never again been seriously questioned. Great thinkers and naturalists had already early documented the similarities between primates and humans. Anthropologists and paleontologists, making use of the analogies to be drawn from the study of extant primates, have endeavored to reconstruct the natural history of humans and primates.

This history often has had to be interpreted from meager evidence. The last decade, however, has yielded many new fossil finds that now allow more detailed insights into primate and human evolution. Primate paleontological, behavioral, and molecular research continue to provide important kinds of clues to this particular type of study. The late development of this field is indicated by the fact that one of the first academic courses in primatology was taught by Elwyn L. Simons as recently as 1959. Elwyn Simons is also credited to be the mastermind of a new field in science: paleoprimatology (Fleagle and Kay, 1994). The field of primatology covers not only the study of primates but ultimately focuses on the human quest to gain an ever-increasing understanding of the most influential of extant primates, *Homo sapiens,* ourselves.

## The future of primatology

The field of primatology covers such varied research areas as anatomy, locomotor behavior and morphology, typology and variation, cell and molecular biology, and genomics as well as primate and hominid paleontology, growth and development, social behavior, taxonomy, reproductive biology and conservation. For example, one major scope within primatology centers on the interpretation of body form and function. Form and function are closely interrelated in the morphology of bones and teeth. By studying the movements of living primates, we can begin to identify the relationship between morphology and function in these mammals. With caution, and within limits, such functional interpretations can (by analogy) be applied to fossil forms to reconstruct the function of extinct animals. This can only be done effectively when we know as much as possible about the lifestyle of present-day species. In fact, even today it would be an exaggeration to imply that we know well the biology of most living primates, but nonetheless the groundwork has been laid. Fundamental studies on the

locomotor behavior of living primates are now being undertaken in increasing numbers and with advancing precision. Modern video and biomechanical technology has made possible more intricate insights into locomotor behavior. The discussion of terminology for basic primate locomotor types continues unabated. This is the case because extant primates exhibit a wide variety of habitat uses and locomotor behaviors. For example, it long seemed impossible to reconstruct with confidence the locomotor behavior of earliest hominids. Now, with new comparative knowledge gained from other living primates and from modern humans we can approach the problem with increasing confidence. There has been a lengthy debate about whether the ancestors of humans, before they became true upright walkers, were brachiators living in the forest canopy or, alternatively, whether they were quadrupedal branch runners and climbers. From fossil finds and comparative studies made in recent years, we have now gained increasing clarification about these alternatives. The supposition that wild gorillas and chimpanzees were brachiators (resembling the small Asiatic gibbons) persisted for a long time in the literature without verification from field observations. In the meantime, long-term field observations have shown that gorillas virtually never move by means of arm swinging and that chimpanzees, as adults, rarely arm swing during locomotion.

Comparative research on a broad range of primates has shown that we are not only very different from other primates in aspects such as bodily proportions and the construction of skull and face but also in our complex way of life. However, biochemical findings of the last few years have indicated great similarities between humans and the African apes, especially the chimpanzee. The intrinsic complexity of a single individual increases as the structural and behavioral organization of animals becomes more advanced. This is especially true for monkeys and apes.

The course of human evolution is now documented by an ever-increasing number of fossils, and there will surely be collections of many more if the search for human forerunners can be continued. The rough outline of the successive phases in the history of humans during the last 3 million years can now be drawn with general agreement. Recent finds appear to have doubled this age to 4 million for the earliest *Australopithecus,* but the period from 2 to 4 million years ago is still not clearly understood. *Australopithecus* has a skull that is outwardly more reminiscent of the apes than that of modern humans, but the teeth are not apelike. There is definite evidence that by about 3.5 million years ago at least, some hominids had already achieved an upright gait.

## Retrospection and prediction

Darwin and some of his contemporaries already recognized that humans and apes were close relatives. Recent research has shown that this resemblance is further evident when one examines the microstructures of these primates. Today a close relationship between humans and apes is reinforced by the most modern methods of cytology, serology, genetics, and molecular biology. It is clear that many characteristics of the human organism differ only quantitatively from other primates. It is, therefore, more the exaggeration of certain characteristics in humans rather than qualitative differences that makes us distinct.

A hypothesis of the Dutch scientist Louis Bolk, who in 1926 suggested that humans are nothing but apes who have retained infant proportions into adult stages, has received broad circulation and regularly resurfaces in formulations of scientific ideas. This speculation that originated with Bolk is fascinating only at first glance. Examples of slow development in the ontogeny of humans, which would substantiate Bolk's theory, can easily be found; for example, the late fusion of the sutures between the bones of the brain case. It is also easy to find examples of speeding up rather than slowing down in human embryonic development, such as the early fusion of the elements of the sternum. When one has the advantage of knowing the developmental history of a broad spectrum of different primates, it becomes obvious that the developmental differences between humans and the other primates are achieved by a combination of speeding up (acceleration) and slowing down (retardation). New research on comparative behavior and cognition of primates, both in adult societies and during the individual's behavioral growth, has changed our thinking. The dependency of the offspring on the mother up to puberty was thought to be unique to humans. Now we know that here, too, we have only differences of degree between humans, apes, and monkeys. Newborn apes show as much need (but for a shorter period) for the mother's care as humans do. Although juvenile development, the learning period, the onset of puberty, and the following phases of life are definitely shorter in apes than in modern humans, all follow the same fundamental sequence. Even newborn monkeys, which are more self-sufficient than infant humans or apes, cannot survive on their own in the wild without the mother—and without the whole troop in many cases. Because young monkeys have much to learn and because, within the troop, experiences are passed from generation to generation by example, we see here the beginning of different traditions varying from troop to troop within the same species.

Young monkeys must practice activities that will be important for their integration into adult social life. During play they come to understand their physical abilities. They learn how to defend themselves, how to help themselves in difficult circumstances, and how to escape. Juveniles isolated from their mothers and from the group do not develop the proper behavioral repertoire for social integration. Such monkeys cannot later develop the capacity for complex social interactions with con specifics.

Thus, the mother and her care are very important during the first stages of life. After this, play with other infants is necessary for later behavioral development. Such findings are important to understanding human behavior and in all attempts to reconstruct possible early human or prehuman behavior. Nevertheless, it is simplistic to suppose that behavioral observations on the nonhuman primates can be used directly to infer the early behavior of humans. Play in monkeys, in human children, or among human ancestors may have, or have had, somewhat different functions. However, using the cladistic view, if play behavior does occur in most primates, it likely occurred in their common ancestor.

Thus, comparative research among primates can demonstrate that human ontogeny after birth indeed has a certain uniqueness. All phases of life—childhood, youth, adulthood, and old age—are absolutely longer in humans than in any other present-day primate. The difference of *H. sapiens* here is particularly marked in the later maturation of individuals together with the continued accumulation of individual wisdom and knowledge, a process on which much of human civilization depends. This long period of old age is a new development in

organic evolution. We all know that the human life span long outlasts the reproductive period, and in fact much of what it means to be human depends on this particular component of human existence.

The living primates provide us with a range of adaptive diversity that by analogy allows us to speculate on the adaptive nature of our ancestors. Thus, the combined field and laboratory studies of primate behavior and adaptations enable us to learn more about our relatives the primates and to enrich understanding of ourselves and our origins.

Primatology has many practical applications. For example, a whole series of biomedical questions have been considered and a variety of medicines and medical procedures were developed through the study of captive primates. Extensive laboratory analysis of primates, especially monkeys, has been devoted to the study of nutrition, infectious diseases, deficiencies of the heart and circulatory system, arteriosclerosis, Alzheimer's disease, diabetes, and cancer. Not the least of their contribution was the involvement of nonhuman primates in the initial stages of space exploration. Thus, our relatives, the nonhuman primates, have been and still are invaluable acolytes in the endeavor to improve human life and self-understanding. In this context we must not forget that judicious care has to be taken to protect our closest relatives from extinction. We must be the guardians of our world, not those who exploit it into oblivion.

Primatologists increasingly raise their voices in warning that the wild populations of many primates are under imminent threat of abolition. Because the survival of our planet's ecosystems is a human responsibility, we must ensure the future of all living organisms and not just our uniquely successful own kind. If lemurs, lorises, tarsiers, monkeys, and apes all should become extinct, we will not only lose the chance to understand further the pathway through which we ourselves arose, we will also turn our world into a bleak and desolate place. Even though natural extinction is not an uncommon event, we alone can avoid being the cause of animal extinction.

Development of primatology in the last 50 years has not only produced new comparative insights but has also shown that there are still many aspects of primate history and biology about which we know very little. Consequently, beyond present understanding, broad topics open up for future research and improved understanding. Primatology today is a vigorous and important science. A distinct separation between ourselves and the most closely related nonhuman primates does not exist. Yet *H. sapiens* stands out as much more than an animal: our species alone exhibits the ability to reason and speak, to write and read, to plan for the future, and to produce civilization, culture, science, and religion. We are also the only primate that has put into jeopardy the future of its own species as well as that of other living things. Human overpopulation may ultimately lead to the destruction of our own living sphere, and consequently to the end of humanity.

Although in biology, evolutionary processes are usually complex and influenced by multiple factors, it appears that there are now two powerful and crucial trends at work on our planet. One is the ever-increasing population of the human species. Humans are a major force that make a plethora of demands on Earth's resources. Glaciers are melting, and temperatures are rising. On the other hand, the human mind has evolved to be able to recognize that we must try to protect the biotic diversity as well as the abiotic components of Earth's environments, such as water, minerals, metals, and energy, from destruction.

Between these two factors—which are mutually irreconcilable—there is an evolutionary conflict in progress, and it is questionable whether the defense of Earth's resources can be sustained under the multifaceted human onslaught. The crucial question, one that will only be answered with time, is whether it will be possible to put the defensibility factor to work soon enough to prevent the extreme outcome of this contest: disappearance of many or most of Earth's biotic and abiotic resources and, ultimately, total self-destruction of the human species.

There is no doubt in my mind that Earth will be just fine without humans, and evolution will restart itself for a new, most likely different and exiting evolutionary adventure in the millions of years to come.

But we won't be around to study it.

## Definition of order primates

The Linnaean order Primates has no doubt stimulated more scholarly and popular interest than has any other major group of mammals. These vertebrates have a long history. Ostensibly, they first appeared in the form of the late Cretaceous genus *Purgatorius,* a genus that was described by a single tooth (Van Valen and Sloan, 1965; K.D. Rose, 1995). In addition to the interest arising from the fact that humans are ranked in this mammalian order is the diversity of the group, which includes 61 extant genera with 252 species compared with more than 200 fossil genera—218 according to Shoshani et al. (1996)—containing 405 species. This living diversity makes it the seventh most populous order of mammals in terms of generic groups; the orders Marsupialia, Insectivora, Chiroptera, Rodentia, Carnivora, and Artiodactyla have more genera than the order Primates. The great generic diversity among primates is emphasized by the high variety of locomotor and social systems, and both systems probably show greater variation within the order than can be found within any other major mammalian group. Adding to this entire series of living forms that provide a sequence of grades of organization (roughly approximating a scale or ladder of nature) are the great variety of fossil genera. There are at least twice as many fossil genera as there are living genera. The number is now over 120 and rising every year with the description of new discoveries from the distant past.

A delineation of the order is difficult because many of the characterizing features are not unique to primates (for detailed discussion, see Martin, 1990). Rather, the definition of the order Primates depends on a shared combination of traits, any one of which can be found independently in other mammalian orders.

Primates can be defined as placental mammals having orbits encircled with bone, clavicles, and flat nails on at least some digits. The brain tends to be large relative to body size and shows a posterior lobe and triradiate calcarine sulcus (situated posterior on the internal aspect of the occipital area of both cerebral hemispheres and said to be typical for most primates) as well as a sylvian fissures (also typical for primates, situated on the outside of the hemispheres

and separating the frontal lobe from the temporal lobe). Typically, in primates there are single offspring and two pectoral (in contrast to abdominal) mammae, but the number of bilaterally paired mammal glands has been recorded to be dependent on the regular number of offspring in a litter (Schultz, 1948; Gilbert, 1986). The innermost digits on the extremities are opposable. Males have a pendulous penis and scrotal testes (compared with scrotum and testes being attached to the lower abdomen or positioned inside the abdomen). All primates have a large caecum. Their cheek teeth tend to be simple and low crowned, often with secondary development of surface wrinkling and upper molar hypocones (Hunter and Jernvall, 1995).

The order Primates has two suborders: Prosimii, the prosimians or premonkeys, and Anthropoidea, anthropoids (or more correctly anthropoideans)—higher primates, including Old and New World monkeys, apes, and humans (Kay and Williams, 1994; Williams and Kay, 1995; Wyss and Flynn, 1995).

Besides these two suborders of the mammalian order Primates, there is another group of mammals, the tree shrews or tupaias (family Tupaiidae), that many authorities (Simpson, 1945; Martin, 1990) formerly classified in Primates. Present evidence—although ambiguous—places them as a generalized side branch of insectivores or as order Scandentia. It is a reflection of the taxonomic uncertainty that has created an order separate from Primates for the tree shrews. They have been removed from the order Primates because they seem to be rather different from primates in having high reproductive rates and because it was unclear which mammals were their closest ancestors. Despite the trend to classify tree shrews apart from the order Primates (see Hill, 1953; Van Valen and Sloan, 1965), little work has been conducted to justify that they are actually closer to other Insectivora, for which the principal subdivisions have long been separate, at least since the Cretaceous period. Even if tree shrews are considered to belong to an order separate from primates, they do indicate fairly closely what we think the Cretaceous forebears of primates looked like. Hence, primatologists have often kept and studied tree shrews together with primate colonies. For these reasons, tree shrews are included in this book, together with our survey of living prosimian primates. For those who wish to consider this question further, see Luckett (1980) and Martin (1990). Despite extensive analysis by many authors, the question of whether to exclude the tupaiids from the order Primates has still not been resolved (Rose, 1995). The three mammalian groups reviewed here can be defined as follows:

1. **Tupaiiformes.** An infraorder (or order) resembling primates in the possession of a number of characteristics, such as having a relatively large braincase, eye sockets rimmed by a circle of bone, and males possessing a pendulous penis. Tupaiids differ from primates in lacking flat nails on any digits, all of which are clawed with the large toe aligned with the other digits; they also differ in having the bony floor of the middle ear composed of a different bone from that which encloses the inner ear. Lastly, they have either premolar-like upper canines or none.
2. **Prosimii.** A suborder of primates differing from tree shrews and other nonprimates because they have a petrosal bulla of the ear, typically a higher degree of orbital frontality, and flat nails on some or most of the digits. Hind limbs are usually considerably longer

than forelimbs. Prosimii differ from Anthropoidea because they have no postorbital closure, but a postorbital bar; no fusion of the metopic suture between frontal bones; and no symphyseal suture between the two parts of the mandibles; these are sutures where closure either does not occur or appears late in individual development. Prosimii are also different because they typically have procumbent lower incisors (or toothcombs) and at least one toilet claw on the hind foot.

3. **Anthropoidea.**[3] A suborder of primates in which eye sockets are closed from behind by bony plates and in which there is midline fusion of the two halves of the mandible and in the forehead of the primitively dual frontal bones into single bones (mandible and frontal). The auditory region is characterized by loss of the stapedial artery, a branch of the carotid artery supplying blood to the brain, and its replacement by a large promontory artery.

[3]The term "Anthropoidea" was first introduced by Mivart (1864), who thus contrasted all higher primates "Anthropoidea" to all lower primates "Lemuroidea." When "Anthropoidea" was elevated to the rank of "suborder" that in turn contained the two superfamilies Ceboidea and Cercopithecoidea, a linguistic quandary was created: the name of any taxonomic group ending with "-oidea" used to indicate a superfamily. The now widely accepted use of "suborder" Anthropoidea with two superfamilies, Ceboidea and Cercopithecoidea, all three ending with the suffix "-oidea," is somewhat perplexing, but adopted in this text: in English taxonomy all rankings above superfamilies may be assigned any suffix.

CHAPTER

# 4

# Survey of living primates

OUTLINE



**New paragraph to be inserted at the beginning of old chapter (3rd edition edition) Chapter 4: "Survey of Living Anthropoidea" that will be newly titled: "Intra-specific Similarity in Extant Non-Human Primate Species."**

Even though primate species are morphologically defined as "same," they are not (Schultz 1963). A.H. Schutz taught and researched intraspecific variability in Primates. As an analogy, I remember that when I was 11 years old and helping a shepherdess taking care of a herd of about 30 sheep, I initially thought they were all alike; only to soon discover that they were individuals. The morphological "species even though primate concept" is based on the dogma that within a species, group individuals are similar to, even identical with each other, and distinct from other related groups. Intraspecific similarity and coincidental variability apply to all and any primate species. One startling example of this reality is humans – all in one species: *Homo sapiens,* in spite of genetic differences.

Humans come in very different shapes: tall, short, long limbed, chubby, scrawny, round, oval, square faced, and many more variable features such as the color of our skin and hair. Last but not the least, there are biological and genetically based sex variabilities that seem to always have caused much controversy, disagreement, concern, disdain, and even hatred and murder. And there are Little people living among us. It is remarkable that there are indigenous Tiny humans in remote areas of the world such as the "Iyeke" in faraway forests of the DR Congo.



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