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Prospects in Primate Biology

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Preface

In recent years the great increase in studies in physical anthropology as well as the paleontology of the more recent periods of geologic time has focused scholarly attention on man's relative and potential ancestors to a new level of intensity. Partially, this has been the result of the effect of the evolutionary theories postulated since 1930 by Huxley, Dobzhansky, and others. As Mayr (1963, Animal species and evolution, p. 637) has stated:

> It was hopeless to try making sense of hominid phylogeny as long as the fossil remains of man's ancestors were considered anatomical "types." . . . The study of the geographic variation of animals and a new insight into the process of speciation have introduced into the study of fossil man new concepts [and]—a great simplification of the general picture.

An understanding of man's rapid mental evolution in the past million years, based presumably on the refinements of speech and tool making, has led biologists and anthropologists into a major field of study—the social organization and behavior of primates. Primate biology gives every indication of being one of the most vigorous and rewarding areas of research although still in its formative stages. One of the charming idiosyncracies of this field of study is that it is

interdisciplinary, that is, it is the proper concern of "so-called" biologists, "so-called" anthropologists, and "so-called" paleontologists. Such an unorthodox area for research can obviously best be performed in unorthodox places, perhaps one reason why Hooton's hope (cited by Napier) that primate biology would become established as a separate teaching division in universities has not been realized. Universities as a whole are largely losing their ability to be innovative, thus putting more pressure on smaller institutions like private laboratories or museums to maintain their fundamental reasons for being. I once characterized the Smithsonian Institution as populated by specialists who were inheritors of a tradition of the "unfashionable in pursuit of the unconventional." The urgent need for studies such as those outlined in this paper is underscored by Dr. Napier's concise account of the rapidly diminishing status of many of the primate species. Conservation is by no means a subject to be ignored by scientists. Environmental studies make conservationists out of the most realistic among us. Primate biology thus becomes one of the most urgent of all interdisciplinary concerns of science today.

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Primate biology as a scientific endeavor is unique inasmuch as it provides a mirror into which man may look to discern the nature of his own species.

Nonhuman primates, occupying an intermediate position between other mammals and man, serve as a constant reminder of the continuity of mammalian life. Thomas Henry Huxley in 1876 expressed the essence of this special primate role:

> Perhaps no order of mammals presents us with so extraordinary a series of gradations as this—leading us insensibly from the crown and summit of the animal creation down to creatures from which there is but a step, as it seems, to the lowest, smallest and least intelligent of placental mammals.

The significance of this relationship between man and the nonhuman primates is—to translate and paraphrase the late Earnest Hooton's happy plagiarism of the poet Terence—that "anything to do with primates is something to do with man." It is inherently probable, therefore, that any basic concept developed in the fields of primate physiology, psychology, or therapeutics, for example, can be applied also to man. This tenet now widely appreciated provides the rationale for the extensive use of primates as experimental subjects in medical and sociological research.

Not so widely appreciated, however, is the urgency of providing rear-guard support for the flying columns of applied primate research.

Perhaps at this point it should be emphasized that there are two main types of primate research that, broadly speaking, can be classified as applied/project-oriented or academic/subject-oriented. Project-oriented research is research *with* primates using them as other laboratory animals are used in order to test the efficacy of a technique that cannot be so tested in man. Subject-oriented research is research *on* primates that leads to a further understanding of their biology and, by the nature of their relationship to man, to the development of hypotheses that can be tested subsequently in a human context. Subject-oriented research, thus, tends to produce results that are seldom of immediate applicability to areas of human health and welfare; they are usually at least one stage removed from medical or sociological usefulness.

The work of Landsteiner and Wiener on the *Rhesus-antigen*, which was later shown by Levine et al. (1941) to be identical with the blood-factor involved in cases of human erythroblastosis foetalis, provides a good example of the value of a "once-removed" type of applicability.

As an example of subject-oriented research, Haddow's (1952) field study on *Cercopithecus ascanius schmidti* may be recalled. This basic research project not only contributed to our knowledge of the ecology and behavior of the redtail guenon, but also it provided the essential background to Haddow's later work on the epidemiology of sylvan yellow fever. The work of Harlow and his associates (1958–1965), of Mason (1965), and of Hinde (1966, 1967) on the affectional systems of monkeys and apes already has had profound repercussions in the areas of child health and development and social psychology. In the field of sociology and social anthropology the zoological perspective (particularly in primate field studies) is leading already to a better understanding of human behavior and human social systems (Tiger and Fox, 1966; Morris, 1967). Subject-oriented research also is often anticipatory as discussed by Riopelle (in press), who recalls, inter alia, that W. S. Hunter developed the delayed-response test in 1913 long before it became useful as a means of measuring function in the frontal lobes in man.

Subject-oriented research requires not only a specific training in primatology (at least at graduate level) but a continuing exposure to an academic environment where peer-contact has the salutary effect of promoting self-criticism and of stimulating intradisciplinary, subject-oriented thinking. Project-oriented research, on the other hand, given good primatological advice at its inception, need not be done in a primate-oriented environment; it can be carried out wherever ap-

propriate laboratory facilities and experienced animal handlers are available.

It is easy to understand why, in a period of political or economic crisis with a premium on pragmatism, the "once-removed" aspect of subject-oriented research does not usually attract much in the way of sympathy or support. This attitude, however, is invoking expediency at the risk of self-immolation. It is precisely in such times that a long-term view is necessary. In a recent article, Leaf (1968) stated: "Emphasis only on applied research in medicine would quickly exhaust the present level of understanding and yield only inadequate solutions to major health problems." In particular reference to primate biology, the need for subject-oriented research is pressing, for seldom in the history of scientific endeavor has any new edifice been erected with so little regard for the nature of the bedrock. In a letter to "Science," Moor-Jankowski (1965) pointed out that the paucity of subject-oriented research in primatology has been due not so much to the lack of support (by funding agencies) as to the lack of competent scientists. This deficiency can be traced to the fact that university training for this fruitful field of research is virtually nonexistent.

The hope expressed by Hooton (1954) that primate biology would become established as a separate teaching division in the universities has not been realized. This is not to say that the subject is not being taught at all—far from it. Primatology always has constituted an important aspect of degree courses in anthropology and is taught in most university departments. Principally, however, the emphasis is placed on primate evolution—and a somewhat anthropocentric approach to evolution, at that. Only rarely, for example, are primate anatomy, genetics, behavior, and serology covered in any detail. Primate systematics and classification seldom, if ever, form a part of the curriculum. Perhaps the complete absence from scientific literature of a student textbook on primatology is the best pointer to the present deplorable state of affaris.

It would seem to be a matter of fundamental importance that in countries where primate research is active and ongoing that there should be centers where teaching and training programs in primatology can be carried out and where future staffing needs of research institutes and primate breeding centers can be catered to.

Considering the enormous national investment in primate research, it seems quixotic, to say the least, not to insure that centers of research are also centers of education. Basic research and education programs are inseparable. The establishment of graduate and undergraduate education programs will bring about a rapid accumulation of the baseline data so urgently needed by research scientists today.

It is not possible to anticipate in detail the direction that future research will take, but, without a shadow of doubt, it will become heavily committed in the areas of child development, and mental, social, and environmental health and behavior. In these fields the experimental animal must be a primate. Information, firmly rooted in biology, will be needed about the behavioral parameters of primates under varying conditions: firstly, in the field in the framework of ecology; and secondly, in artificial environments ranging from the near-normal conditions of the field-cage to the wholly artificial conditions of the laboratory. These studies of naturalistic and "semi-naturalistic" behavior are subject-oriented just as certainly as are the more traditional academic disciplines of anatomy, taxonomy, and phylogeny.

Primate Biology Today

The last ten years have seen the coming of age of two subjects concerned with the science of man—human biology and primate biology. Although they can scarcely be considered new disciplines, they reflect a new attitude of mind and provide fresh ways of looking at old problems.

The approach to both is naturalistic. The animal, whether man or nonhuman primate, is studied primarily as a living creature in the context of its normal environment; it is regarded as a member of a natural population, not as an individual; and it is regarded as an expression of the phenotypic variation of the species rather than as the archetype of the race. These principles require new and liberal perspectives in study methods. Human walking, for instance, one of the more simple components of human behavior, cannot be investigated merely by studying the osteology of the limbs, nor can it be explained solely in terms of the biomechanical functions of the relevant muscle groups. Walking also is concerned with the environment of men who walk and with their physiological needs in a variety of different habitats; it is concerned with the effects of culture on the periodicity of this human activity and the historical conditions that led to its evolution.

To study primate behavior entails a consideration of anatomy, physiology, biochemistry, ecology, ergonomics, paleontology, anthropology, and genetics. With a multidisciplinary approach of this sort, primate biologists cannot afford to be specialists. While inevitably possessing special knowledge in particular fields, they require a general awareness of all relevant fields. In this context "awareness" can be interpreted as an attitude of mind that, in turn, can only evolve from a training that is designed to develop it. There is much to

be said for the training of the specialist with his rigorously channelled expertise, providing that his future employment asks no more of him than this; but there is a real place in twentieth-century science for the multidisciplinary scientist.

The interrelationship of primate and human biology is intricate and important both pragmatically and philosophically. They stand in much the same relationship, for example, as political economy and political history, as mining engineering and petrology, as sociology and social anthropology. The first of each pair is concerned primarily with the present, and the second is involved principally with the past. Primate biology, though not a historical subject per se, stands in historical relationship to human biology. Man is a recent innovation of primate phylogeny with a relatively brief history as *man* but an extremely ancient one as a *primate*. Chimpanzees and gorillas are the living descendants of the same group from which man's remote ancestors were drawn millions of years ago. In this regard they serve as genetic models for man. Their value for biomedical research depends on this close blood relationship. Other primates—the baboons, for instance, which, like man, are recent innovations—are too phylogenetically remote to serve as genetic models. Baboons and macaques occupy a broadly similar ecological niche today as the primate precursors of man occupied some fifteen million years ago. The study of these animals, which can be regarded as ecological models, might, therefore, be expected to provide valuable clues for the development of hypotheses concerning the roots of the human social organization. It is no coincidence that baboons, macaques, and chimpanzees are the most widely used of all nonhuman primates in biomedical and sociological research.

The past of organisms is one of the determinants of their future, and the most fruitful place to look for man's past is not only in ancient and inaccessible rocks but also in the structure and behavior of living primates.

At Oxford, England, in 1864 Disraeli said: "The question is this: is man an ape or an angel? My Lord, I am on the side of the angels." A hundred years later we are no longer interested in the answer to Disraeli's rhetorical question. We do not regard it as being particularly important. Man and apes are part of one zoological order, the Primates, an order that also includes the monkeys and the lemurs, and the close relationship of these forms to man is no longer a matter of dispute or concern. The essential conformity of man and the primates in morphology, physiology, serology, and behavior is beyond question, and the problem now facing primate biologists is the clarification of the relationships within the order, with extension of knowledge in depth and breadth to include as much information on struc-

ture, genetics, behavior, and ecology for as many different species of primates as possible.

Professor Sir Wilfrid Le Gros Clark in an address to anthropologists in 1959 discussed the evolution of a new discipline. He observed that all branches of science in their neonatal stages passed through a collecting and cataloging phase. As far as primate biology is concerned, these preliminaries must be regarded as an essential stock-taking exercise during which the language and methodology of the subject must develop and the basic facts of primate biology are collected, synthesized, and disseminated. Primate biology is still, strictly speaking, in this phase. We still need to find out what it is all about, what we know, what we don't know, what is relevant, and what is totally irrelevant. Primate biology needs a plan, a blueprint from which to build a significant and durable structure.

Diminishing Primate Stocks

High on the priorities list of a primate research program should be studies directed toward the understanding of the *captive* primate. Before the end of this century there will be only a few natural populations of primates, living undisturbed lives, left in Africa, Asia, or Latin America. The majority of nonhuman primates will be captive in one sense or another. They may be under close restraint in medical laboratories, in zoos, in breeding ranches in the tropics, in free-ranging colonies in temperate zones, on isolated islands, or in reservations and game parks, but captive, nevertheless. This gloomy prognosis is the inevitable result of extrapolation from three unrelated trends: firstly, the ever increasing deforestation that results from agricultural development in tropical countries; secondly, the widespread native habit of killing monkeys for food, particularly in West Africa, where they constitute a vital source of animal protein; and thirdly, the exorbitant rate of consumption of primates by research scientists. Importation of monkeys into the United States during F.Y. 1966 has been estimated to have exceeded 100,000 individuals; the vast majority, it can be assumed, ended up in biomedical research laboratories. This rate of consumption could lead rapidly to extinction of certain populations in the wild: monkeys simply do not breed at this rate. Rhesus monkeys and the common langur (*Presbytis entellus*) already are showing signs of depletion in certain regions of Asia. Southwick, Beg, and Siddiqi (1961), who carried out a population study of rhesus monkeys in 1959–1960 in the Uttar Pradesh province of India, observed a marked shortage of juveniles in many troops.

The golden tamarin (*Leontideus rosalia*) is said to be near extinction in Brazil although the blame in this instance cannot be laid at the

door of the scientist. In Sierra Leone it has been estimated that, for every young chimpanzee exported for research or for zoos, between four and six mothers have to be killed. Since each of these mothers might be expected to produce up to ten offspring in a lifetime, the potential loss to the wild population for *every* young chimpanzee captured is between forty and sixty individuals. Estimations of this sort can never be particularly reliable, but even the loss of a single breeding female for every infant captured could eventually have a severe effect on population numbers.

There are clearly several ways of approaching the problem of diminishing primate stocks. Firstly, there is the matter of conservation. This is an admirable concept, and, indeed, conservationists can chalk up a number of important successes for which the whole world should be grateful, but unless the aims of conservation are anticipatory rather than retrospective, the problem of the primates will not be solved by such measures. The only possible procedure for the orangutans of Borneo (it seems inevitable that the Sumatran race is past saving) is to establish protected colonies on suitable islands. The real problem for the future are monkeys such as the patas, the vervet, the baboon, and the macaque, all of which, though plentiful now, may not always remain so. On the basis of present trends, it is difficult to see how natural populations of these animals can survive beyond the end of the century. It is the *potentially* vanishing species that should be the principal targets of conservationists, not populations that are already doomed.

Information is urgently needed on the population numbers of free-ranging primates, particularly the most popular laboratory animals, in order to guide future policies on importation of primates and the establishment of breeding colonies at home. We have little or no precise knowledge of current wild population numbers or of population dynamics in the countries of origin of these animals. Rumors abound, but factual information is lacking.

Choice of Primates in Medical Research

Although the literature in recent years on the care of primates in medical research laboratories has grown astronomically, relatively little consideration has been given to the selection of primates specifically appropriate to particular types of research investigations.

The choice of a nonhuman primate is largely a hit-or-miss affair and will continue to be so until the biological properties of all species have been fully investigated. Reference to recent publications (e.g., Montagna, 1967), to the symposium volumes edited by Vagtborg (1965) and Fiennes (1966), respectively, and to the textbooks of

Ruch (1959) and Fiennes (1967) would reveal a great deal of information on the proved and potential usefulness of particular species for particular problems. A comprehensive account of the research potential of the 197 species of primates is beyond the scope of the present article.

Choice of a suitable primate for a specific project, therefore, must depend on hearsay, on the published reports of other workers, or, in the last instance, on trial and error. Finally, selection will be influenced by pragmatic considerations that relate to available space, available resources, and available primate species. There are no hard and fast principles by which suitable animals may be selected except that of phylogeny, which, at best, can act only as a general guide.

The phylogenetic article of faith is simply stated: The experimental results that are most likely to be meaningful in a human context are those carried out on animals that have the closest genetic relationship (and, therefore, phylogenetic proximity) to man.

The phylogeny of the primates is shown diagramatically in figure 1, wherein primate families and their component genera have been arranged in terms of their relative closeness to man.

PROSIMIANS.—The Prosimians comprise six families, which are arranged as follows: Tupaiidae, Lorisidae, Daubentoniidae, Indriidae, Lemuridae, and Tarsiidae (Napier and Napier, 1967). The use of prosimians as laboratory animals has been discussed recently by Manley (1967), Montagna (1967), and Hill (in press).

Treeshrews (Tupaiidae) are not unequivocally primates. Opinions differ strongly at the present time as to whether they should be so regarded. The attitude taken by the author is that, whether technically they are primates or not, they are thought to be so close to the phyletic root of the order (at a time when all primates were insectivores, so to speak) that they should be retained in the Primates, if only as a permanent reminder of the generalized mammalian origins of the stock. Treeshrews have not been used widely as laboratory animals except in strictly physiological experiments, but with the new information emerging on breeding behavior (Martin, 1966), they may well attract more attention.

Among the Lorisidae, galagos are potentially the most useful. Their relatively short gestation period (*Galago crassicaudatus:* 130–135 days; *G. senegalensis:* 144–146 days) and the not uncommon occurrence of twin births mark them as possibles. A number of primate centers and research laboratories are breeding these animals successfully. The melanistic race, *G. c. argentatus*, is tougher and heavier than the brownish *G. c. crassicaudatus* and may prove to be more hardy in captivity; it is possible that it may be a good subject for an open-air colony situation.

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The Lemuridae are the only other family of the Prosimian radiation that are likely to be available for laboratory work; the remaining families are too rare and too delicate to be considered. Lemurs, specially the robust ring-tail (*L. catta*), have been bred successfully

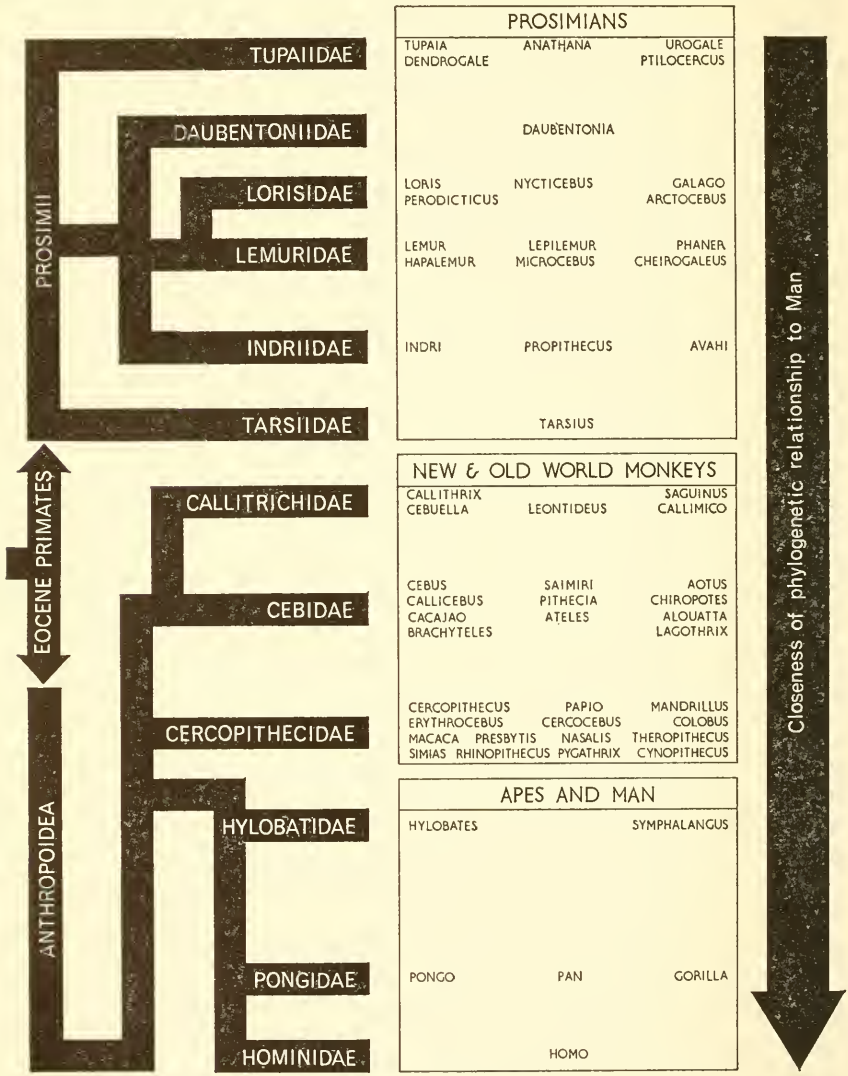

FIGURE 1

in quite large numbers in laboratories and zoos in recent years as also, to a lesser extent, have the black lemur (*L. macaco*) and the brown lemur (*L. fulvus*); however, it is certain that scientists who have a special reason for employing these animals in research will have to

depend wholly on their own breeding stocks in the future as all Madagascan prosimians are rigorously protected. The value of prosimians as laboratory animals is largely unknown, but, generally speaking, their usefulness lies in the field of basic research. This is exemplified by the ongoing studies of Montagna and his colleagues on cutaneous anatomy and physiology. As substitutes for higher primates in the fields of cancer research, immunology, and pharmaceutics, they leave much to be desired.

New world monkeys.—The New World monkeys comprise two families, the Callitrichidae [1] and the Cebidae. Marmosets (*Callithrix*) and tamarins (*Saguinus*) have enjoyed—if that is the right word—a high popularity during the last five years. Their principal advantage is their small size and the free availability, in particular, of *Saguinus*. The common marmoset (*C. jacchus*) is becoming increasingly rare according to certain authorities (Hill, in press).

A discussion of the suitability, disease hazards, and basic biological data of marmosets and tamarins has been summarized by Deinhardt and Deinhardt (1966); breeding of marmosets in captivity has been discussed by Hampton et al. (1966).

Although phylogenetically the most remote from man of all higher primates—and, therefore, of limited value in procedures that hinge on close genetic proximity to man—marmosets are most useful animals in certain specific research projects. In the study of viral hepatitis, for example, they appear superior to other nonhuman primates, always excepting the expensive chimpanzee (Deinhardt and Deinhardt, 1966).

Among the Cebidae, the only species that merit consideration at the moment are the squirrel monkeys, the douroucoulis or night monkeys, and the capuchins. The shortness of this list reflects as much as anything the neglect of the New World genera by primate biologists. No doubt this neglect can be traced to the remoteness of this group from the story of human evolution, which in the past constituted the principal raison d'être for studying primatology.

Cebus, the capuchin, which is said to be resistant to tuberculosis, has been discussed by Stare et al. (1963), principally in relation to dietary factors in the etiology of atherosclerosis. Squirrel monkeys, which fulfill nearly all the criteria for the ideal laboratory animal except that of phyletic proximity, are widely used in neuroanatomical studies in arteriosclerosis research and in space physiology. One of the most surprising animals to emerge as a promising laboratory species

[1] The spelling of Callitrichidae is that originally used by Thomas (1903). The termination appears to be formed in accordance with Appendix D, Table 2, of the "International Code of Zoological Nomenclature" (1964), and, therefore, there is no case for amending Thomas' spelling.

is *Aotus* (the douroucouli), the only nocturnal higher primate and one of the most primitive monkeys in existence.

Old world monkeys.—The Old World monkeys comprise the single family Cercopithecidae; of the two subfamilies, the Colobinae and the Cercopithercinae, only the last named are presently of interest to the research scientist. The contribution of the Cercopithecinae to human research has been discussed by Jolly (1966).

Macaca mulatta, the rhesus monkey, the "monkey" of medical literature, is too well known to merit discussion here; its use in the identification of the Rh blood factor and in the development of poliomyelitis vaccine is common knowledge. The breeding record of the rhesus macaque, its toughness, availability, and cheapness make it the best all-round research animal. Certain other macaque species as the crab-eater, the pig-tail, the stump-tail, the bonnet, and the Japanese macaque all breed well in captivity. The last mentioned promises to be especially valuable as a species that can be bred freely in open-air compounds, even in high latitudes.

The closely related Celebes black "ape" (*Cynopithecus niger*) is another primate that seems to breed well in captivity. As a bonus, Celebes apes are, for Old World primates, quite friendly animals. One might guess that imported stocks of *Cynopithecus* are never likely to be adequate for extensive research usage due to the restricted range of the species. Their future usefulness will have to depend largely on domestic breeding programs.

Baboons have grown in popularity in recent years and are becoming biologically very well documented (Vagtborg, 1965). They are of particular value in surgical procedures (Moor-Jankowski, 1967). Baboons have been used extensively in studying the etiology of atherosclerosis and other cardiovascular diseases of man at Sukhumi in the U.S.S.R., for instance, and at the Southwest Foundation, San Antonio, Texas.

The leaf-eating section of the Cercopithecidae, the Colobinae of southeast Asia (*Presbytis, Nasalis*, etc.) and Africa (*Colobus*) are so specialized in their diet and, relatively speaking, so little known biologically that they have no place in medical laboratories at the present time. A possible exception to this generalization is the Hanuman or entellus langur (*P. entellus*), which is hardier than most other species and more ground adapted (Jay, 1965).

The remaining Old World monkeys to which reference should be made have been grouped by some taxonomists (Jolly, 1965) into a tribe, the Cercopithecini, that includes the following genera and subgenera: *Cercopithecus*, *Cercopithecus* (*Miopithecus*), *Cercopithecus* (*Allenopithecus*), and *Erythrocebus*. This tribe is not generally regarded as important in biomedical research, but there are at least three

species that are worthy of note—the talapoin, the savannah monkey,[2] and the patas. The talapoin is untried as a laboratory animal but is theoretically desirable in view of its small size and the possession of a sexual swelling in females. Savannah monkeys have been used fairly extensively, notably in the culture of poliomyelitis vaccine. Patas monkeys are used quite widely in Britain today; the fully adult male patas monkey, however, equals a male baboon in size.

Some slight success in breeding talapoins in the laboratory has been reported (Hill, 1967). There is little information on breeding of patas monkeys beyond the fact that between 1959 and 1963 twenty-four births were recorded in world zoos (Napier and Napier, 1967). Goswell and Gartlan (1965) have recorded a single instance of a laboratory birth. Savannah monkeys and their allies, on the other hand, breed moderately freely. It seems logical to anticipate that other members of the genus *Cercopithecus*, such as *C. ascanius schmidti* (the red tail), would be of value in research once they are better known biologically.

Apes.—It is hardly necessary to discuss the apes in the context of human research. While it is obviously highly desirable on phylogenetic grounds that chimpanzees should be used for many aspects of biomedical research, their expensiveness and relative rarity should preclude their use other than in very exceptional circumstances wherein no alternatives exist. This does not prevent chimpanzees from being employed in experimental work that does not result in the sacrifice of the animal. It is perhaps in the fields of functional morphology and growth and aging studies that these animals can contribute most to human understanding.

Gorillas and orangutans have no place in the medical laboratory owing to their extreme rarity although, as in the case of chimpanzees, they can contribute to many aspects of human biology. The only remaining ape species to be considered is the gibbon. Being the most active of all primates, they require considerable space in order to remain healthy through the performance of a normal locomotor repertoire. Their unique—in an Old World primate sense—social behavior patterns make them unsuitable as breeding animals.

The scientist faced with a research problem must choose the animal most suited to his requirements. Perhaps the most serious question that he must ask himself is: Need primates be used at all for this particular experiment? Would not a white rat, a guinea pig, or a rabbit do just as well? The conservation of wildlife is a serious scientific, economic, and social problem and not simply a hobby for elderly ladies. Primates are rare animals, and it should be a matter for pro-

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[2] Common names of the three geographical species of the savannah monkey (*C. aethiops* group) are the grivet, the vervet, and the green monkey.

found thought before the decision is made to remove an animal from the wild. Medically useful primates must be bred in captivity in sufficient numbers so that the cause of scientific conservation is not imperilled by the extravagant demands of a sister science.

Primate Biology at the Smithsonian

This recently inaugurated primatology program has a single, clear purpose: To foster the development of primate biology as a scientific endeavor on an international scale. It is to be hoped that this new program will play a central and a catalytic role in the rapidly expanding field of primatology by encouraging basic research, particularly in systematics, and promoting educational programs in the universities, particularly those closely associated with centers of primate research.

The Primate Biology Program is planned as an international facility having, in the first instance, two offices, one in Washington, D.C., at the Smithsonian Institution, and one, in London, England, with close affiliations to the University of London. For geographical and other practical reasons it is likely that the program emphasis will differ somewhat between the two centers; for instance, the magnificent collections, the preparation and storage facilities of the U.S. National Museum, and the proximity of other major museum collections would favor Washington as the locus of systematics research. On the other hand, the close association of the London office with the University of London will facilitate the development of this center as a locus of undergraduate teaching. Graduate training programs would be located in both centers; however, it is not envisaged that the various projects will be divided between the two centers so much as shared between them. Each will contribute to the total program as its native talents and material resources dictate. A regular exchange of students and professional staff between London and Washington will do much to foster the principle of unity.

The following section constitutes a working plan that embodies a research and education program of considerable magnitude and breadth. It is not anticipated that all the projects will develop simultaneously; indeed, it may be several years before some of them can be initiated.

Research Program

Certain aspects of primate biology such as systematics and nomenclature, anatomy and physiology, evolution, zoogeography and population dynamics, free-ranging behavior and ecology, and base-line data on the ecology of captivity are in urgent need of development. These problems are the basic requirements of research workers who, in the design stage of their experiments, must ask themselves a series

of questions (the particular fields of study that might be expected to supply the answer are shown in parenthesis):

Q. 1. Which is the most suitable primate for my purpose? (Anatomy, physiology, psychology. Evolution. Systematics and nomenclature.)

Q. 2. Where can I obtain a regular supply of this species? (Zoogeography. Population dynamics.)

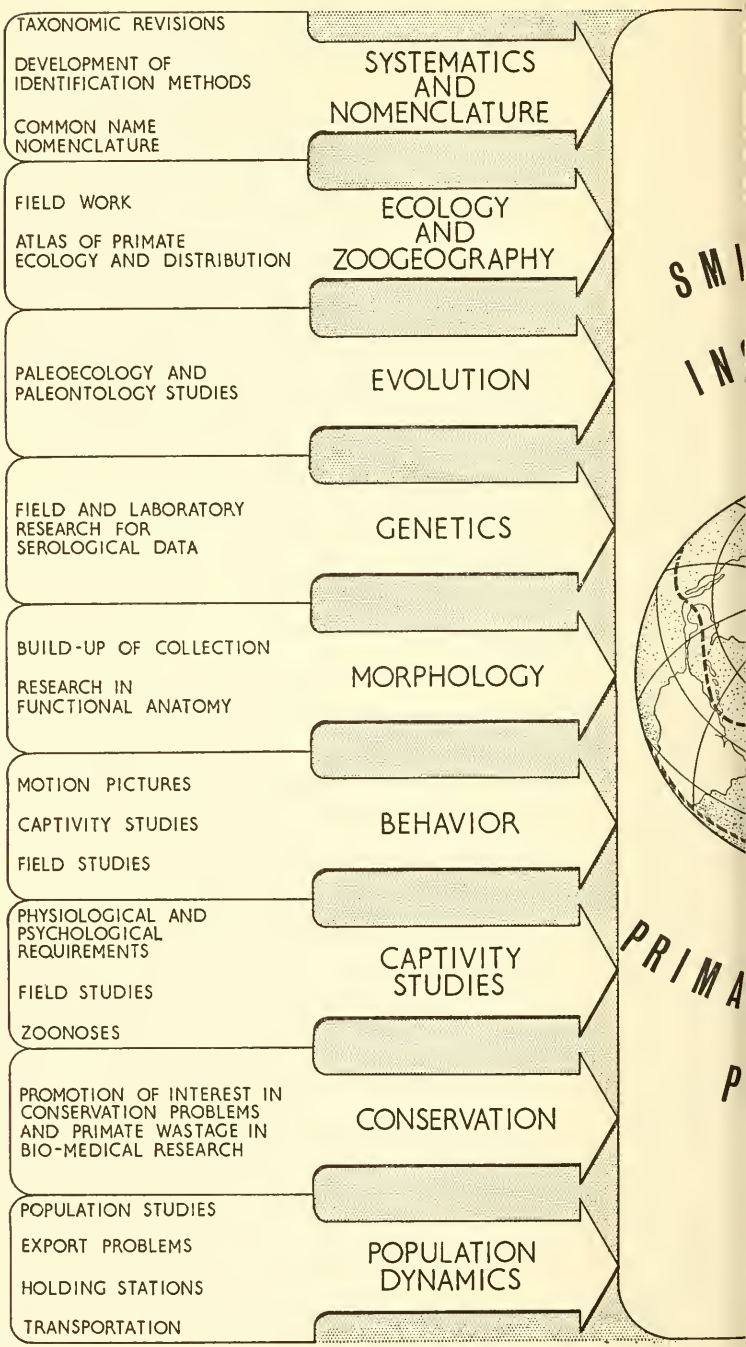
Q. 3. How can I best maintain these animals in captivity? (Free-ranging behavior and ecology. Base-line data on captivity ecology.)

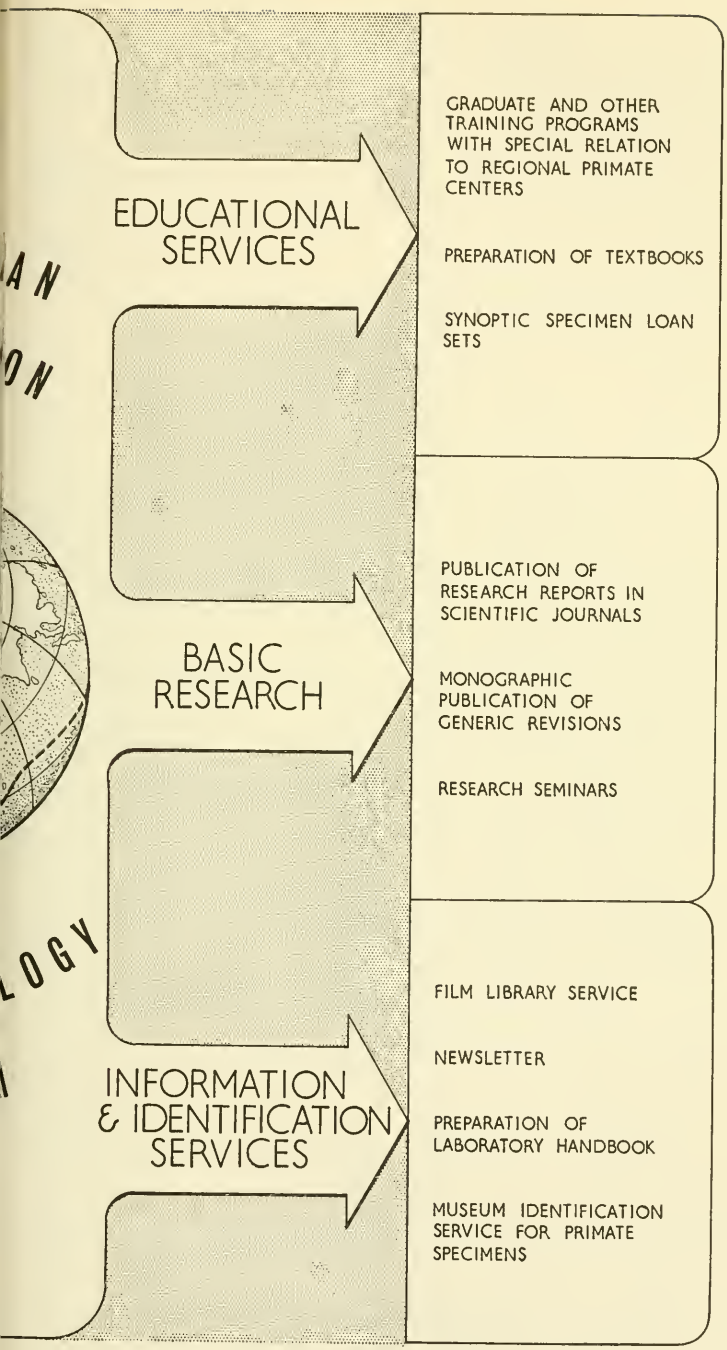
It is in such fields of inquiry as these that the Smithsonian Primate Biology Program will concentrate its efforts.

PRIMATE SYSTEMATICS.—Problems in primate systematics are many and great and constitute a major handicap in the rapid development of research programs employing nonhuman primates as experimental animals. The interpretation of results in fields of physiology, pharmacology, psychopathology and neuropsychiatry, comparative psychology and ethology often depends on a precise knowledge of the systematic status of the subject animal. With imperfect identification, the contributions of previous research workers cannot be utilized, experiments cannot be repeated, and hypotheses—dependent on the precise knowledge of relationships—cannot be developed or tested.

A revision of primate systematics is long overdue for many groups and should rank high in the priorities of any program. Research in primate taxonomy should start with revision of genera. It is difficult to talk about species within a genus without knowing the exact limits of variations among genera themselves. Genera in most urgent need of revision, other than those already being examined, are found in most of the prosimians, many of the Cebidae, certain Cercopithecidae (particularly *Cercopithecus* and *Cercocebus*), and all the Colobinae. Only after restudying such genera can classifications be revised in a meaningful way. Many of these lists are half a century or more old and include species and subspecies that, in the light of modern theories, are quite invalid. The use of computers and advanced statistical techniques are providing new and more accurate means of zoological classification. A recently (Groves, 1967) completed study of gorilla populations using these techniques is an example of the sort of results that can be obtained. Evolutionary studies are a necessary component of systematic revisions; for example, the arrangement of higher categories of Old World monkeys depends on understanding of the phylogenetic relationships among the *Macaca-Papio* ground-living group of Old World monkeys, the arboreal colobine monkeys, and the curiously intermediate *Cercopithecus* and *Cercocebus* groups.

Inasmuch as modern systematics is based on the total biology of populations, a program of revision must be broadly based and must


TAXONOMIC REVISIONS
DEVELOPMENT OF IDENTIFICATION METHODS
COMMON NAME NOMENCLATURE
SYSTEMATICS AND NOMENCLATURE
FIELD WORK
ATLAS OF PRIMATE ECOLOGY AND DISTRIBUTION
ECOLOGY AND ZOOGEOGRAPHY
PALEOECOLOGY AND PALEONTOLOGY STUDIES
EVOLUTION
FIELD AND LABORATORY RESEARCH FOR SEROLOGICAL DATA
GENETICS
BUILD-UP OF COLLECTION
RESEARCH IN FUNCTIONAL ANATOMY
MORPHOLOGY
MOTION PICTURES
CAPTIVITY STUDIES
FIELD STUDIES
BEHAVIOR
PHYSIOLOGICAL AND PSYCHOLOGICAL REQUIREMENTS
FIELD STUDIES
ZOONOSES
CAPTIVITY STUDIES
PROMOTION OF INTEREST IN CONSERVATION PROBLEMS AND PRIMATE WASTAGE IN BIO-MEDICAL RESEARCH
CONSERVATION
POPULATION STUDIES
EXPORT PROBLEMS
HOLDING STATIONS
TRANSPORTATION
POPULATION DYNAMICS


EDUCATIONAL SERVICES
GRADUATE AND OTHER TRAINING PROGRAMS WITH SPECIAL RELATION TO REGIONAL PRIMATE CENTERS
PREPARATION OF TEXTBOOKS
SYNOPTIC SPECIMEN LOAN SETS
BASIC RESEARCH
PUBLICATION OF RESEARCH REPORTS IN SCIENTIFIC JOURNALS
MONOGRAPHIC PUBLICATION OF GENERIC REVISIONS
RESEARCH SEMINARS
INFORMATION & IDENTIFICATION SERVICES
FILM LIBRARY SERVICE
NEWSLETTER
PREPARATION OF LABORATORY HANDBOOK
MUSEUM IDENTIFICATION SERVICE FOR PRIMATE SPECIMENS

involve research into many diverse fields of primate biology such as anatomy, paleontology, behavior, serology, and genetics. Thus, the systematics program undoubtedly will provide a considerable mass of fall-out information in these special fields of study in addition to providing taxonomic revisions of the genera.

Priority from the point of view of early revision will be given to those genera most commonly used in scientific research. The marmosets are undergoing revision at present (Hershkovitz, 1966, and in litt.) as are some of the macaque species (Fooden, 1964, 1967). *Papio* recently has been restudied, principally from the viewpoint of osteology and paleontology (Jolly, 1965).

The genus *Cercopithecus*, on the other hand, has not been fully revised since Schwarz' (1928) study, although Hill (1964, 1966a, 1966b) has contributed much toward our knowledge of the taxonomy of these animals, particularly from the point of view of gross anatomy. Certain species and species-groups such as the Mona monkeys have been reviewed recently by Booth (1955); and the *aethiops* group, by Dandelot (1959). Verheyen (1962) has studied the skull osteometrically and osteologically; Chiarelli (1966) has supplied a great deal of information on chromosome numbers. Jacob and Tappen (1957, 1958) have studied haemoglobins. Booth (1956, etc.) has studied the ecology of certain West African representatives, and Haddow (1952) has supplied detailed information for a single subspecies, the redtail (*C. ascanius schmidti*). Few behavior studies have been published; Hall and Gartlan (1965) have observed the social behavior of *C. aethiops* on Lolui Island, Lake Victoria, and Cynthia Booth (1962) and Brain (1965) have studied the behavior of certain species of *Cercopithecus* in captivity. These studies must be extended to include all twenty-one species and sixty-seven subspecies now recognized. It must also be extended to the closely related forms *Miopithecus* (the talapoin, a species potentially of great value to research on account of its small size), *Allenopithecus* (the swamp monkey), and *Erythrocebus* (the patas monkey) with a view to determining whether these forms are congeneric with *Cercopithecus*. The *aethiops* species-group of *Cercopithecus* are another potentially important source of laboratory primates. The aspects of the biology of this group needing particular study are serology, ecology, and behavior. Evolutionary studies, which should provide the basis of any classification, are also most important (see Jolly, 1966); fortunately, the fossil material of the Cercopithecidae is moderately common, particularly in the Pleistocene (Jolly, 1965). A zoogeographical study of the group after the manner of Hershkovitz on *Callicebus* (1963) is also imperative for the full understanding of their origin and dispersal (see also Tappen, 1960). It is proposed, therefore, to initiate a revision of the genus *Cercopithecus*. Other

genera to be studied early in the program will include *Saimiri* (the squirrel monkeys) and *Presbytis* (the langurs).

Taxonomic Teams: Revisions of the systematics of any group cannot, and should not, be carried out by any one individual. Essentially, these are team projects that should reflect the multidisciplinary approach of primate biology. For the proposed fundamental revision of the genus *Cercopithecus*, a team consisting of specialists in the following fields will be co-opted and will operate under the general direction of the author:

1. Osteometric and osteological studies.
2. Serology.
3. Locomotor adaptations.
4. External characters.
5. Ecology.
6. Behavior.
7. Evolution and zoogeography.

Other scientists will be co-opted on an ad hoc basis to study various special aspects of the program, i.e., parasitology.

Duration of Project: In view of the proposed depth and breadth of the revision of *Cercopithecus*, it seems likely that the project will last at least three years, possibly four or even five. Since the systematics team will be drawn from suitably experienced scientists working in different parts of the world, it is considered essential that they should be in constant communication in order that the products of their different viewpoints can be closely coordinated. As far as is possible, a new systematics project involving a separate team will be initiated every second year. Thus, at the end of a five-year period the revision of three important primate genera will be underway.

Study Conferences: The majority of the scientists comprising a "taxonomy team" will be employed on a consultant basis. In order to facilitate close coordination on the project, annual study conferences will be held to bring together the scientists concerned either in Washington or in London.

Publication: During the course of the project, publication of the results of individual studies will be encouraged. At the conclusion of the project, the revision will be published as part of a monograph on the biology of the *Cercopithecus* group.

Nomenclature.—Revision is needed also in primate nomenclature. As more and more medical research laboratories utilize primates, the more urgent becomes the problem. The present nomenclature of primates is neither adequate nor sufficiently stabilized for scientists to communicate with one another without considerable danger of misunderstanding. The common laboratory primate, the crab-eating macaque, is a classic inmate of the nomenclatorial madhouse. It is widely and incorrectly known as *Cynomolgus* and less widely, and cor-

rectly, known as *Macaca fascicularis*, although most current systematic lists refer to it as *Macaca irus*. It is understandable that harassed research workers should throw up their hands at such an impossible situation and end by using its unequivocal common name, the crab-eating monkey. The stability-loving primate biologist asks nothing more than that he should be able to retire at night with a name on his lips that is still valid when he wakes up in the morning.

A Study Group for Primate Nomenclature and Systematics Research will be established at the Smithsonian under the aegis of the Primate Biology Program. Its purposes will be twofold: immediate and long-term. The immediate aim will be to prepare, in the light of present knowledge, the best possible working list of primate species for use in the Primate Centers and other research laboratories; its long-term function will be to determine the areas of primate biology where systematics research is most urgently needed, to foster such research, and to revise critically the nomenclatorial list from time to time as new, irrefutable evidence becomes available. In this way it is to be hoped that primate nomenclature will achieve a *uniformity* in primate research that it has never before enjoyed. Total *stability* of nomenclature is something that cannot be guaranteed; to advocate such a procedure would be to deny the ebb and flow of scientific opinion. Stability, nevertheless, will be the watchword of the Study Group and purely technical name changes will be examined very critically before the status quo of the working list is disturbed.

Laboratory identification.—The identification of animals at specific and subspecific level is a fundamental need in both the research laboratory and in the museum. The simplest method is by means of external characters. In the event, considerable reliance is placed on coat coloration. The only means by which this can be achieved other than by direct comparison with known specimens is by reference to published descriptions. Many of the current descriptions antedate the introduction of the Ridgway color system and are, therefore, unstandardized. The earlier Munsel system has been little used in mammalian identification. Even post-Ridgway descriptions with their innumerable subtypes (1115 in all) of the named colors of the spectrum are so complex as to be almost useless in practice for the taxonomist and nontaxonomist alike. At best, all qualitative systems are subjective.

It is proposed to investigate the feasibility of developing a quantitative method of determination of coat colors using the technique of "reflectance spectrophotometry" (Dice, 1947; Hill, 1960). There are a number of techniques available for color specification: the spectrophotometric curve, the tricolor reflectance value, and the C.I.E.

(Commission Internationale de L'Eclairage) system, which provides evidence of the dominant wave length of samples.

A pilot study of *Saimiri* is already underway. Hopefully, this technique will provide a method that can be used by nonprimatologists and primatologists alike to aid in the identification of the species under investigation.

POPULATION DYNAMICS.—Information is urgently needed on the population numbers of free-ranging primates, particularly the most popular laboratory species, in order to guide future policies on importation of primates and the establishment of breeding colonies in temperate climates. We have little or no precise knowledge of current wild population numbers or of population dynamics in the countries of origin of these animals.

Primate population studies should provide information on population levels, population trends, export problems, holding stations, transport mortality, as well as local attitudes and customs involving primates that might affect exportation.

This is a major project and will need to be developed in two phases: (1) The basic background knowledge of the distribution, abundance, and population dynamics will be gleaned from what is already published in the literature on primates. Much of it is archaic and imprecise, but, nevertheless, there is much that is of value that should be collated as a first step. It will be possible to extract much information on distribution, less on abundance, and very little on population dynamics. (2) Following library research, there should be corollary field studies of several of the important species. Primary emphasis would be on the definition of ecological factors most critical in limiting population growth and those factors favoring population expansion and maintenance. Means of carrying out censuses of populations in various situations would be sought. Finally, model studies of the population dynamics of one or two important species should be undertaken.

Much of the field work in the preliminary stages could be carried out in certain of the soft-currency countries under the Smithsonian's Foreign Currency Grant Program.

STUDIES OF THE HUSBANDRY AND WELFARE OF CAPTIVE PRIMATES.—One approach to the problem of diminishing stocks discussed above is obviously the increase of breeding and holding programs in artificial environments. Much more basic research is required before such programs can supply all the animals of different species that scientists require. One must know, for example, the normal diet of the primates concerned, as well as its seasonal variations, and the typical locomotor habits and resting postures of the primates in order that appropriate

cages, enclosures, holding chairs, etc., can be designed. One must understand the social composition of the species concerned; each species has its own pattern of social behavior that must be understood if the animals are to be kept in captivity as healthy breeding units. One must know the technical details of the microclimate, the temperature-ranges, and the humidity. One must know the physical nature of the environment: Do these monkeys live among the small flexible branches of the canopy, on the stout branches near the trunk, or on the trunk itself? Only by finding the answers to these questions can one hope to provide, artificially, something approaching a realistic (though obviously not a normal) environment for the animal concerned. To provide a captive animal with an adequate, suitable environment is not only humane but sound common sense. Many of these problems are now being tackled in the Regional Primate Centers in the United States, but the basic research necessary for a full awareness of the welfare and husbandry of a wide range of primates will take many years of detailed and imaginative research.

Boredom in captive primates is another very serious, but generally unappreciated, problem. In the wild, most of the primate's working hours are spent in search of food. If, in captivity, it is deprived of this occupation, it has no normal substitutes. It develops behavioral aberrations such as coprophagy, masturbation, and stereotyped behavior patterns like staring into space for long periods, clasping the head or body and rocking to and fro, and hopping from one foot to another. These are typical withdrawal patterns seen in deprived primates, human or nonhuman. It has been said that "a solitary chimpanzee is no chimpanzee at all." Much of the boredom can be alleviated by caging monkeys in social groups so that normal social interactions, such as grooming activities among adults and play among infants and juveniles, can help to compensate for the lack of active food-getting. Ideally, some type of food-getting activity should be devised; for example, it should be possible to mix food pellets or natural food objects into the deep gravel or sandy floor surface of the day cage in order that the animals can spend many hours of the day digging and hunting for food. In this way an element of uncertainty and variety can be introduced into the daily life of the animal. Higher primates need, above all, intellectual employment and the stimulation of unusual objects or events.

The principal aim of the research will be to obtain measurements of tolerance of monkeys to captive conditions in laboratories, zoos, and in "free-ranging" captivity. The following aspects of tolerance should be considered:

1. Climatic: Response to high and low temperatures and humidity levels; habitus changes associated with different climatic conditions.

2. Physical Environment: Responses to altered environmental situations demanding changes in locomotor habits, resting habits, spacing behavior, sexual behavior, aggressive behavior, etc.

3. Dietetic: Responses to wide range of food and feeding patterns, with particular reference to changes in the skeleton.

4. Social Organization: Study of ideal group size in differing captivity situations and its relation to cage size.

5. Diversionary: Investigation of the value of "spare time" activities in the general welfare of the captive.

An essential correlate of this program will be a field investigation of certain basic behaviors of primates in the wild, e.g., diet, locomotion, climatic tolerance, resting posture, etc. (see "Field Studies" below). Captivity studies are clearly a long-term project that will be based both in the United States and the United Kingdom. Informal talks already have been held with a pharmaceutical research center in England that is interested in the possibility of setting up primate research of this general nature on its estates in the South Midlands.

Field studies.—Field studies of free-ranging primates are pivotal to the systematics, captivity, and population studies discussed above, and they will constitute an important part of the program.

It is hoped that it will be possible to establish junior and senior field-study studentships for graduate as well as post-doctoral scientists. Senior studentships normally would be held for five years and the junior appointment for three years. This period will ensure that the post-doctoral worker will, on the completion of his field work, be available to contribute to the systematics and captivity research projects and to the teaching and other activities of the Primate Biology Program. A policy might be adopted whereby the holders of these two studentships would act as senior and junior members of a field-research team.

The possibility of establishing a field primate research training program at the Smithsonian Tropical Research Institute, Barro Colorado Island, Panama, in connection with the award of the junior field-study studentship will be investigated.

Functional anatomy.—Collection of data on sound biometric principles is still an important part of primate biology. There is no better example of this type of work than that provided by Adolph Schultz, whose lifetime study of growth and variability in the skeletons of higher primates has contributed so much to our knowledge. Statistical techniques such as that of multivariate analysis will in the future provide an even better method of assessment of such data; furthermore, it is expected, as a fall-out from such projects as systematics research, that new information on the anatomy and physiology of primates will become available. The field of primate anatomy has

been developed industriously for the past hundred years by authorities too numerous to mention. A synthesis of a century's work is admirably recorded in the monumental treatises of Dr. W. C. Osman Hill of the Yerkes Regional Primate Center. The physiological, or functional, anatomy of primates has attracted less attention. Because of its relevance for primate behavior, the anatomical and physiological whys and wherefores will rate special attention. The "new" science of Lorenzian ethology, in particular, seems to the writer to require an injection of what Elliot-Smith called the "illumination of comparative anatomy"; it is somewhat paradoxical to study the evolutionary significance of facial expression in primates, for instance, without a detailed understanding of the function of their facial musculature.

Over the years a number of projects in functional anatomy have occurred to the writer and are listed below. These are random ideas and are in no sense a definitive list of research proposals.

1. Significance of cheek pouches in primates.
2. Phylogeny and physiology of sexual swelling.
3. Anatomy, social significance, distribution, and phylogeny of sexual dimorphorism.
4. Adaptive significance of the bulla tympanica.
5. The relationship of the fat pad under the heel of primates to ecological adaptation.
6. The anatomy and behavioral significance of swimming in primates.
7. The functions of the primate tail.
8. Adaptations of the vertebral column in relation to primate locomotor patterns.
9. Adaptations of the nails and their phylogenetic significance.
10. The carriage of infants in relation to the locomotion of primates.
11. The functional morphology of ischial callosities.
12. The neonatal coat color; its significance in natural selection.

Education Program

In the earlier part of this paper considerable emphasis has been laid on the multidisciplinary approach of primate biology and on the need of its students to acquire a versatile attitude of mind. Primate biologists, for instance, who possess a working knowledge of systematics are to be preferred to systematicists who have a working knowledge of primates, for the systematics of primates should be based on the sum total of their biology, past and present.

The greatest deterrent to subject-oriented research in primate biology is, undoubtedly, the lack of primate biologists. The Smithsonian will not only supply grist for its own mill, but also it will provide a service for other museums and research institutions by developing an education program in this field.

Cooperative Graduate Programs: It is anticipated that the Smithsonian will be seeking education agreements for cooperative graduate

programs with certain universities in special relation to centers of primate research. Schemes of this nature would involve praticipation by staff specialists in lectures and seminars held at the graduate school in question and the admission of graduate students to internships at the Smithsonian for a period of a year or less under the supervision of staff members.

Crash Courses: Short and intensive courses on the principles of primate biology will be arranged for institutions and research centers for the benefit of professional employees and technicians.

Undergraduate Courses: Lectures and seminars will be arranged under educational agreements with universities in association with anthropology and zoology degree courses. In order to implement such educational agreements, the permanent professional staff, term appointees, graduate students, and consultants in specialist fields would be expected to play a professorial as well as a research role. Although the academic level of the different courses will vary with the status of students concerned and with the nature of their scholastic background, the subject content will be fairly constant and will embrace the following fields of study:

Principles of evolution, systematics, classification and evolution of primates. Zoogeography and ecology. Anatomy, physiology and behavior with particular reference to habitat (anatomical and ecological basis of behavior). Molecular biology and genetics. Zoonoses, welfare and husbandry of the captive primate. Conservation.

Courses will comprise some lectures but principally seminars and practical classes. Motion picture film will be used extensively (see "Film Library" p. 26). An essential corollary of a teaching program is the production of a comprehensive textbook. This obviously cannot be conjured up overnight and it may be several years before a satisfactory student manual can be produced. As an interim measure, the author is preparing a short student text that should be available, modestly priced, in 1969.

Collection Programs

The nature of the program outlined above will necessitate, above all, large and adequately cataloged study collections of primate skins, skulls, skeletons, and wet specimens.

Data Processing: Participation in the Automatic Data-Processing System for cataloging and retrieving information relating to specimens, a system already in use in the Museum of Natural History, is a possibility to be investigated. It is questionable whether the size of the present collection of Primates in the Division of Mammals would justify the high cost involved. Considered in terms of the international orientation of this program, however, such a partici-

pation would seem highly desirable; accordingly, the Primate Biology Program will consider the feasibility of processing data relating to primate collections in the major museums of the world. A project of this sort would be inconceivable for such organizational units as the Department of Invertebrate Zoology or the Division of Ornithology, but for the Primate Biology Program, which is concerned with relatively fewer species, a world-wide catalog is not out of the question. Such a catalog housed in one institution would be of immense value to primatologists.

Augmentation of Collection: Few museums possess sufficient duplicate material to allow synoptic loan-kits of skulls and postcranial bones to be made available to accredited institutions or to permit wet specimens to be dissected by graduate students; yet, such facilities would form an important part of an education program. Efforts will be made to augment the Smithsonian's already extensive collections by various means so that the following services can be implemented:

1. Specimens for Dissection: At present there is no adequate collection of embalmed specimens suitable for detailed anatomical dissection. Many requests for such material reach the Smithsonian annually. In the course of building up systematic reference collections, stocks of properly preserved anatomical material should be developed. These stocks would serve as a "bank" from which specimens could be drawn for study.

2. Whole Specimens for Loan: It is proposed to build up a "library" of the common varieties of primates. The animals preserved in their entirety would be stored in polythene envelopes without fluid and would be available for loan to scientific institutions.

3. Synoptic Osteological Collections: For temporary loan to primate centers and other scientific institutions.

4. Film Library: For certain fields of study, motion pictures are the essential correlate of more formal methods of instruction; for example, in primate biology, with its emphasis on behavior, films should comprise a major part of the course. It is not easy with large classes to demonstrate behavioral experiments on primates in the laboratory, but the identical experiments can be presented to any number of students simultaneously through motion pictures. Ecological and behavioral studies in the wild are assuming great importance in primate biology and naturally constitute a major part of student instruction; it is clearly impossible to transpose a group of students to the rain forest but perfectly feasible to bring the rain forest to them—on film. Locomotion studies are pivotal to the understanding of primate biology for the primate is structurally a locomotor machine. Locomotion can be illustrated theoretically in a biomechanical diagram of forces, but its behavioral significance, in relation to feeding, etc., can be understood only in dynamic terms where posture, movement, and environment are brought together in one demonstration. It is proposed to develop a library service lending films to laboratories and university departments for educational use. This is substantially the procedure that is followed at the present in the Smithsonian Unit of Primate Biology in London.

5. Identification Service: The existing collections of the Division of Mammals would make it possible to provide an identification service for outside organizations.

6. Identification Manual: There would appear to be an urgent need in many laboratories that use for a short and concise identification manual; preparations for such a publication are already underway. The manual would incorporate a number of color plates of the skins of certain common laboratory primates.

Postscript

A long time has elapsed since 130 A.D., when the anatomist Galen of Pergamum, discovering that, of all living things, the ape is "likest to man," proceeded to practice what he preached by using monkeys as substitutes for human cadavers. Eighteen centuries later—although the correctness of Galen's pronouncement has long since been proven up to the hilt—we are still somewhat chary of admitting the full potential of this relationship.

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