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ANATOMY OF THE HAND IN CATARRHINE MONKEYS AS RELATED TO MANIPULATIVE BEHAVIOR

by

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A dissertation submitted to the
Graduate Faculty in Anthropology in
partial fulfillment of the requirements
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CHAPTER I. INTRODUCTION

The Cercopithecoidea have been studied since antiquity (McDermott, 1938; Morris, 1966; Hill, 1966). In his history of animals, Aristotle wrote down his observations on what has been identified as the Barbary Ape (Morris, 1966). While Pliny later added some details to the work of Aristotle, the subsequent anatomists relied on previously written material, and tended to misinterpret or exaggerate statements, so that by the time of Galen (130 A.D.) knowledge of the Cercopithecoidea was quite confused (McDermott, 1938). Galen's _Anatomical Procedures_, which were largely done on baboons and Barbary apes, became the standard texts on primate anatomy in Europe for the next 150 years.

A widespread medieval view of the Church since the fall of Rome, was that the ape was evil (McDermott, 1938; Morris, 1966). During the Renaissance, monkeys lost their evil connotation and came to be regarded as fools rather than devils (McDermott, 1938). This attitude ushered in a period of renewed interest in cercopithecoids. One of the earliest studies of this period is by Leo Africanus (1550) who told of his travels in Sudan and adjacent regions of Africa, including vivid anecdotal accounts of _Cercopithecus mona_ (McDermott, 1938). Although much of the writing during this period was compilation and borrowing from earlier sources, some important empirical work was done by

Vesalius. He presented evidence that Galen had based his studies on apes and not humans, thereby encouraging further comparative studies (Morris, 1966).

While Renaissance artists such as Pieter Breughel the Elder and Teniers portrayed various species of Cercopithecus on canvas, the royalty of Europs maintained menageries whose specimens provided material for comparative anatomy as well as behavioral data.

At the very close of the 17th Century, Edward Tyson's important comparative anatomy appeared. "The Anatomy of a Pygmie Compared with that of a Monkey, an Ape and a Man" (1699) is cited frequently as being pivotal in primate studies (Huxley, 1863; McDermott, 1938; Hill, 1966; Morris, 1966). It was the first good comparative anatomy (Huxley, 1863), reliable enough to be used as reference by such scholars as Primrose (1899) and Gregory (1930). Although this study concerned monkeys only parenthetically (Huxley, 1863), it introduced a period of objective scientific interest which soon encompassed monkeys as well as apes. This interest in the Cercopithecoidea was, until the time of St. George Mivart, largely as a stage in the evolutionary progression towards the apes and on to man. St. George Mivart raised some doubts as to the irrevocability of man's descent, common or linear, from or with the apes (1871, 1874). His criticisms, coupled with the iconoclastic contributions of F. Wood-Jones, opened a new path for speculation and research. At first arguing that man was in an anatomical sense equidistant from all other primate groups (1916), Wood-Jones (1919) later showed that the ancestral stock of man might have been like a Tarsier.

Both Mivart and Wood-Jones were severely criticized in their times, the former by Darwin and his allies (Gruber, 1960), the latter particularly by Hooton (1930) and Gregory

(1930). The impact of Mivart's and Wood-Jones' contributions was not diminished by these criticisms. Their virtually heretical statements served to stimulate younger researchers to re-examine the entire primate order, the current doctrines of its phylogeny, and theories of its arboreal and terrestrial adaptations.

By the 1930's, cercopithecoids were being used as laboratory animals because they were closer phylogenetically to man than typical laboratory mammals, and more available than the great apes. Interest in rhesus macaque, for example, was sufficient to have introduced nearly 13,000 of these animals into the United States by 1936 (Carpenter, 1940). The use of cercopithecoids as laboratory animals resulted in anatomies of single species such as Hartman and Straus' Anatomy of the Rhesus (1933), and more recently, in laboratory manuals like that of Berringer, et al. (1968). Primate centers conducting research primarily on Cercopithecoidea have been established throughout the world. Added to those in the United States, Russia, Africa and Japan, are the ones under construction in Germany and France. These centers conduct studies primarily in biological and medical sciences, including physiological aspects of behavior.

Other than the two anatomical monographs of the rhesus cited earlier, there are no complete works of this kind of other genera of the Cercopithecoidea. Osman Hill's handbook on the Primates includes a volume on the Cercopithecoidea, but as it is a compendium of all subjects pertaining to these animals, the sections on anatomy and behavior only touch on the major features of each genus.

The more advanced non-human primates are set off from the other mammals by the nature of their communication systems and their dependence on the forelimbs for manipulation. While the functional anatomy of organs relevant to communication in catarrhine monkeys has been extensively described (e.g., Andrew, 1963; Hockett, 1964; Altmann, 1966; P. Reynolds, 1968), a review of the literature shows that although there are numerous papers on locomotion including Cercopithecoidea (Anthony, 1912; Bishop, 1964; Ashton, et al., 1965; Tuttle, 1967; Oxnard, 1963; Jouffroy & Lessertisseur, 1960) and a number on the form of the cercopithecoid hand in general (Midlo, 1934; Schultz, 1930, 1950; Jouffroy & Lessertisseur, 1960), very little has been done on the use of the forelimb in manipulation. The works of two authors are noteworthy exceptions: behavioral studies by Alison Bishop (Jolly) on the Prosimii (1962, 1964), and papers by J. R. Napier since 1955 which have concentrated on the functional anatomy of the hand of non-human primates. Napier believes that one of the factors most influencing the evolution of man has been his ability to manipulate objects. He recognizes that this ability has depended on the complex movement termed "opposition." While Haines credits du Bois Reymond (1895, 1896) with the first analytic statement of the functional anatomy of opposition, Kaplan (1953) the translator of Duchenne, cites his important work of 1858, acknowledging however, that it was little known until recently (1949). Both scholars defined opposition as a combination of movements - flexion, abduction and rotation occurring at the carpometacarpal, metacarpophalangeal and interphalangeal joints, which rotate the thumb on its longitudinal axis so that the palmar surface of the tip comes in contact with the palmar pads of the other digits.

Opposition was understood to begin from a central position, that is, a position midway in the circumduction of metacarpal I., rather than the anatomical position, which is not a true functional position and which leaves ambiguities as to muscle direction. This central position, is equivalent to the "position of rest" defined by Ellis (1878) in clinical practice (Napier, 1960) and which has become a standard position for evaluating the action of the three joints of the pollex (Wood-Jones, 1920; Haines, 1944; MacConaill, 1946; Kaplan, 1953; Napier, 1960). Later researches into the anatomy and function of the non-human manus as well as the human, utilized the early definition with little refinement (e.g., Schultz, 1926; Ashley-Montagu, 1931; Haines, 1944; Le Gros Clark, 1959; Napier, 1960; Jones, 1967). In these writings it is assumed that opposability and opposition are synonymous. Napier, the foremost living student of the non-human primate hand, in his

1961 paper concerned with the phylogeny of manipulative ability in non-human primates, perpetuated this confusion when he defined "Opposability as a from of prehensility where the converging pollex undergoes axial rotation" (p. 118) and further on defined opposition as "... a compound movement of abduction, flexion and medial rotation occurring at the carpometacarpal articulation of the pollex" (p. 119). However, in his most recent work (1967, and personal communication), he has restricted the term opposability to properly refer to the potential or ability for the movement, "...by which the pulp surface of the thumb, undergoing flexion and rotation at the carpo-metacarpal joint, can be placed squarely in contact with or diametrically opposite to, the pulp surface of one or all of the remaining digits" (p. 397). This most recent definition of opposition is in accord with the surgical view reflected by Kaplan (1953) evaluating the role of the three joints of the thumb as a minor one. Kaplan, while admitting that the motion of opposition is "enhanced" by lateral angulation of the proximal phalanx at the metacarpophalangeal joint, argues that opposition of the thumb is due to motion only at one joint - between the 1st metacarpal and the trapezium)p. 233, 1965). However, an earlier definition (Napier, 1966) and the studies and experiments of Joseph (1951), Landsmeer (1957), and McFarlane (1962), have shown that activity at the carpo-metacarpal, metacarpophalangeal and interphalangeal joints are responsible for opposition.

Statements accepting opposability as an attribute of cercopithecids have been current since the late 1920's (e.g., Schultz, 1926; LeGros Clark, 1959; Rasch, 1963; Campbell, 1966; Hill, 1966). The purpose of this paper is to evaluate the frequency and limitations of this ability. Napier has noted that opposability varies in the Cercopithecidae with the habitat as a gradient from ground to tree. However he has only examined two aspects of opposability and both of these are osteological: (1) the ratio of the length of the thumb to the second digit which he names the Opposability Index, and (2) the palmar concavity of the carpal canal which is a function of the articulation of the trapezoid with the scaphoid.

My intention is to evaluate (1) the behavior of opposition, (2) its frequency of opposition, and (3) the circumstances of this behavior in several species of <u>Cercopithecus</u> heretofore completely unstudied. Furthermore, my intention is to isolate (4) the mylogical and osteological variables affecting opposability in these species, and (5) to correlate these data with the habitats and feeding behavior of these species and to compare them with other genera of Old World monkeys.

The thesis is a synthesis of behavioral and anatomical researches. Most of the data were gathered in Africa at the Tigoni Primate Research Centre. Tigoni was chosen because:

(1) several species of Cercopithecus and other genera of Cercopithecoidea were present permitting intraspecific and intrageneric comparisons;

(2) animals were grouped in large cages permitting interactions;

(3) they were fed unprepared foods, therefore approaching the wild condition, and they manipulated these foods spontaneously.

(4) Tigoni is situated in the countryside and is not very far from locations where groups of Cercopithecus are free-ranging.

Further investigations were continued at four primate centers in the United States: Holloman Air Force Base, Delta Regional Primate Center, Sterling Forest Primate Center and the Regional Primate Center of the University of Washington. Although these four centers do not include populations of the genus _Cercopithecus_, some species of _Papio_ and _Macaca_ were accessible for limited comparison with _Cercopithecus_ species. These comparisons included dissections and experiments with picking food from a tray, but precluded observation of fully spontaneous manipulative behavior as the animals were caged singly and fed prepared foods in a hopper or cup.

Six species of Cercopithecodea were studied at Tigoni: four of _Cercopithecus_ and one each of _Erythrocebus_ and _Colobus_. The four species of Cercopithecus were: _C. mitis_

C. ascanius, *C. neglectus* and *C. aethiops*. The *C. mitis* include two subspecies, the Sykes and the blues (C. Booth, personal communication). They are listed in Hill (1966) as members of the Superspecies *C. mitis*, Wolf, 1922 as -- Sykes -- *C. albogularis kolbi*, Sykes, 1831 (Plate XIV and XV) and - blues - *C.m. stuhlmanni*, Matschie, 1893, Plate XIII).

These four species were chosen as the core of the study, because they have similar types of locomotion but differ in their use of the hand in feeding. These animals are all forest dwelling plantigrade quadrupeds. *C. ascanius*, *C. mitis* and *C. neglectus* prefer wetter, denser forests than do *C. aethiops* who regularly occupy drier or fringe forest zones and are found in savanna as well (Haddow, 1952; Tappen, 1960; Booth, 1962; Hall, 1965; Struhsaker, 1967). While *C. ascanius* and *C. mitis* exploit the forest canopy and are, for this reason, arboreal, *C. neglectus* and *C. aethiops* utilize the resources of the ground both for food and migration, although they sleep in trees and conduct other life activities there (Booth, 1962).

Two other genera of the family Cercopithecidae were available at Tigoni and are included for comparative purposes as both species exhibit adaptations to a restricted habitat: *Erythrocebus patas* to the savanna floor and *Colobus abyssinicus* to the forest ceiling. *E. patas* is closely related to *Cercopithecus*, and was first placed in that genus in 1907 by Pocock who later reconsidered (1925) (Hall and Mayer, 1966). While Verheyen (1962) has urged the inclusion of this group within *Cercopithecus*, recent students have retained the generic name *Erythrocebus* (Hall and Mayer, 1966).

Both *E. patas* and *Colobus abyssinicus* exhibit locomotor specializations; indeed, *Colobus abyssinicus* is a semi-brachiator (Oxnard, 1963) and *E. patas* often assumes a digitigrade posture, particularly when running. *M. mulatta* occupies a habitat in India similar to that of *C. aethiops* in Africa; that is, it is equally at home on the ground or in the branches, and is known from the drier forest regions (Pocock, 1932; Southwick, *et al*. 1961 ; 1965; Neville, 1968). *P. doguera*, like *E. patas* is a terrestrial animal, considerably adapted to savanna (Devore and Hall, 1965).

The next section on methods outlines how the behavioral and anatomical researches were carried out. The behavioral aspect includes (1) observations of how the hand was used under ordinary circumstances in procuring and manipulating food items including frequency counts for the hand positions, or grips in the natural repertoire, and (2) experiments involving feeding at primate centers in the United States. The anatomical aspect entails (1) measurements of articulated and disarticulated hands (2) dissections of fresh, frozen and fixed specimens and (3) still and moving pictures both negative and x-ray.

CHAPTER II. REVIEW OF THE LITERATURE

On the Anatomy of the Hand in Catarrhine Monkeys

Anatomical descriptions of single specimens of Pongidae and Mivart's researches into the morphology of the Lemuroidea dominated the Darwinian era to 1880. In that year Bischoff's monograph appeared. It was a study of the significance of the extensor indicis proprius and the flexor pollicis longus in the comparative anatomy of man and apes. Bischoff noted that the flexor pollicis longus is occasionally absent in man as Wagstaffe had earlier shown (1872), but is more consistently lacking in the hands of the great apes. In a later paper, with Walsham, Wagstaffe presented a human anomaly similar to the typical monkey condition, that is, fusion of the flexor profundus digitorum with the flexor pollicis longus (1880).

Testut (1883) noted that the antievolutionists since the time of Gratiolet and his school had used the fact of the absence of the flexor pollicis longus-whether total or as an independent muscle in apes and monkeys-to substantiate their position. He felt that his work, however, coupled with Wagstaffe's and others, refuted the antievolutionists by showing that the non-human primate condition appeared in man.

Studies on the mechanics of the human hand, the first by Braune in 1887, became more frequent in the 1890's and early 1900's. DuBois Reymond's monographs of 1895 and 1896 (Haines, 1944) discussed phalangeal movements in man and gave a detailed account of the joints involved in opposition. Reymond defined this movement, and saw that it involved all three pollical joints. While studies comparing the joint mechanics of man and catarrhines were published at this time (Keith, 1894a), similar studies on the joint mechanics of the non-human primate hand did not appear until the work of Schultz (1926) and later Ashley-Montagu (1931). These scholars measured the length of the thumb against the third digit. Schultz (1930) found that the pollical index might vary within genera and Montagu (1931) believed that it might have ecological and phylogenetic importance.

In 1902, McMurrich published his Phylogeny of the Forearm Extensors, but a similar work on the flexors was not published until 1941 (Straus). While both these studies dealt with the comparative anatomy of the respective muscle groups in primates, McMurrich was concerned with the notion that they represented stages in the evolution of the antebrachial muscles of man. In the early 1930's, several papers appeared on the myology of primates as such, without reference to man. These were in phylogeny (Miller, 1932), myology (Howell and Brazier, 1931) and gross morphology

(Midlo, 1934). Midlo's paper was extremely important in that it went against previously accepted concepts of generalized and specialized structures in the forearm. He found that of all the primates, the hands of prosimians were the most specialized, while the Old World monkeys were the least so.

A decade later, an interest in the functions of the hand and foot was reflected in much of Straus' work on their biomechanical aspects. In 1944 Hughes' monograph on the transverse carpal arch appeared. It was an analysis of the phylogeny of the carpus and of its function as well. In the same year Haines and Wheeler's paper on the mechanism of rotation appeared. Although this study concerned movement in the human hand, its concepts and data were later utilized in analyses of the primate hand in the work of Napier (e.g., 1960, 1966).

Landsmeer's papers in the 1940's and 1950's have been essential to an understanding of the tendons and joints and the movements permitted by them.

While the past two decades have seen continued interest in comparative anatomy (Haines and Wheeler, 1950; Jouffroy and Lessertisseur, 1957-1960; Day and Napier, 1961; 1963; Lewis, 1965) the primary interest has been in functional anatomy, as is seen for example, in the work of Joseph (1951) who investigated the movements permitted by the structure of the metacarpophalangeal and interphalangeal joints of the thumb in man. Subsequently, McFarlane (1962) concentrated on the action of the intrinsic muscles, and Stack (1962) constructed models to analyze digital movement. More recently, specialized studies of the hand have tended to appear in volumes largely or wholly dedicated to primate locomotion, such as the 1963 Symposium of the Zoological Society of London (no. 10), edited by J. Napier, and the November issue (1967) of the American Journal of Physical Anthropology.

Yet even these recent papers have dealt primarily with the great apes, and with the hand as a mechanism for locomotion. These studies have continued to document the thesis of Keith (1894a) that, "The differences in the ligamentous structure in Man, Anthropomorpha, and Cynomorpha are due to adaptations for their different postures and modes of progression." Studies focusing on the primate hand as a manipulative rather than locomotor organ are few, with J. R. Napier the major contributor since 1952. Napier's work has been largely to define the movements of the hand, surveying the primate order. Since his interest is in phylogeny, Napier's analysis of opposability in Old World monkeys contrasts the entire genus _Cercopithecus_ with _Papio_ and _Macaca_. In a 1960 paper Napier earnestly called for further studies on the use of the hand (p. 656). Allison Bishop Jolly's work on prosimians (1962, 1964) and Tuttle's on the great apes (1967) remain the sole exemplars of such studies. A few *Cercopithecus* species were cursorily treated as comparative to the prosimians in Jolly's two studies. Jolly used eight species of *Cercopithecus* at the Bronx Zoo and studied their manipulative behavior by means of experiments. These included requiring the primate subjects to remove raisins from narrow necked bottles, in order to evaluate the mobility of the second digit. Her conclusion that the second digit in *Cercopithecus* species does not move independently from the other digits is not confirmed by the present study.

A few papers on motor innervation and spindle afferents to motorneurones in baboons have just appeared (Clough, *et al.*, 1968; Eccles, 1968) but no further studies of functional anatomy of the hand in species of *Cercopithecus* have yet been published.

Field Observations of Functional Anatomy

Although much field work of many species of primates has been undertaken since the 1930's (Zuckerman, 1932; Pocock, 1932), very little of the resulting data have been concerned with the use of the hand, even in terms of locomotion. The students of the living pongids - Carpenter (1940), Schaller (1963), Goodall (1965), the Reynolds (1963; 1965), Harrisson (1960), and Kawai (1959), include chapters or sections on such functional anatomy in their respective works. Field work on cercopithecoids is more recent, and has focused for the greater part, on genera easily observed, so that the majority of studies are on *Papio* spp. and *Macaca* spp. The concern of these studies is behavior, including social organization, maternal care, communication and the like. While most of these studies include ecological descriptions and analyses (e.g., Imanishi, 1957; Furuya, 1962; Altmann, 1962; Kummer, 1963; Devore and Hall, 1965; Simonds, 1965; Southwick, *et al.*, 1965; Suzuki, 1965; *et al.*) very few interpret the anatomical adaptations the primate has made to its ecology.

Major exceptions to this behavioral emphasis are Jolly's recent work (1966) and Hall's (1962) study of the chacma baboon. While numerically few studies exist on the two genera of the Cercopithecidae mentioned above, there are even fewer on the more elusive *Cercopithecus* species. Haddow's 1952 studies on *C. ascanius* included some ecological considerations (i.e., diet, predators, home-range). Nevertheless, neither his work nor that of Buxton (1952) on this species, nor Struhsaker's work on the *C. aethiops* (1967) deals with anatomy in terms of the environment. Hall's (1966) paper on *E. patas* reflects the more recent trend of interest in functional anatomy as there are sections which endeavor to analyze and relate the environment with certain anatomical features unique to the *E. patas*.

CHAPTER III. METHODS

Behavioral Data

Observations

Observations were the major source of information for the present studies. They were the means by which opposability, that is, the capacity to oppose could be recognized. Eating patterns were especially noted since procuring, manipulating and conveying food items to the mouth elicit the animal's natural repertoire of hand positions and of hand movements. Descriptions of these manipulations focus on the hand not as a platform, strut or hook as in locomotion, but as a tool.

Observations were made at the Tigoni Primate Research Centre nearly every day, at different times of the day, and most consistently at morning and evening feeds over a period of six months in 1966. I was stationed from a point of contact with the cage to a distance of eight feet. The duration of observation averaged three or more hours per day. Free-ranging troops of C.mitis (Sykes) and C.aethiops were studied in the environs; the C.mitis at Thika, a gallery forest, 26 miles northeast of Nairobi, for a total of 6 hours in three visits. C.aethiops were observed in the Nairobi Park for 10 hours in three visits. These studies were facilitated because this park is in savanna and the troop lives around a water-hole. A pair of 8 x 24 field glasses were used and photographs and movies taken occasionally throughout the study.

The Sample - Tigoni: In total, seventy-six live animals were studied at Tigoni: eight *Colobus abyssinicus*, ten *Erythrocebus patas*, four *C.ascanius*, twenty-seven *C.mitis* (twenty Sykes, seven blues), thirteen *C.aethiops*, sixteen *C.neglectus*. Adult males were available for all species except *Erythrocebus patas*. A complete breakdown of the sample by age and sex appears in Table 7. The age categories were made on the basis of behavior. All categories are described below even though "infant" and "juvenile" were not included in the study in order to eliminate the variable of motor control and to insure that the animal had been born in the wild.

INFANT is defined as an animal from birth until relative independence from the dam, that is, until it regularly spends approximately 60 per cent of its time at least a few feet from the mother's body and solid foods become the major part of its diet.

JUVENILE bridges the age gap between infant and subadult. It has greater motor control than an infant and consequently, is more inclined to leap, run and play. It spends most of its time with its peers, but still seeks the dam in stress situations. It sleeps close to, but not necessarily grasping its dam. Some juveniles, especially of the Sykes variety, were noticeably dependent on their dams. They continued to be carried by them even after their size made this behavior cumbersome. This dependency appeared to result from confinement in a cage. It was not encountered in the free-ranging groups of this species observed in the Nairobi City Park and at Thika.

SUBADULT is approaching adult size but still lacks adult bulk (Booth, personal communication). It plays less than a juvenile although more than an adult.

ADULTS are animals who have attained full size and bulk. The females spend most of their time grooming and caring for the young, while the male is primarily the recipient. Neither male nor female adults initiate play, although they tolerate the games of the young which often include the adults as objects.

Sexual exploration is frequent at all ages except infancy. It is at first random, but with increasing maturity, contact is sought more specifically with animals of the same age and opposite sex.

<u>The Sample - Primate Centers in the United States</u>: The sample of living animals observed at Holloman Air Force Base, Sterling Forest and Delta Regional Primate Center includes 20 adult <u>Macaca mulatta</u> and five adult <u>Papio doguera</u>. As these animals were observed while they remained in their

single-unit cages, no observation other than counts of specific manipulative positions were made. A breakdown by species, age and center appears in Table 10.

The Setting - Tigoni: The animals lived in outdoor cages, aligned in rows. The dimensions of the cages were 12' x 8' x 8' except for the *Colobus abyssinicus* whose cage was 14' x 24' x 12' (Booth, personal communication). Each cage was equipped with shelves and bars, which afforded sleeping places. While these latter also served as exercise furniture, a rubber tire suspended from the ceiling by a metal chain was included in each cage. One wall of the cage was wooden, the others wire mesh, the squares of which measured 2 inches (10 cm.). The floor was concrete. The cages were almost completely exposed to the elements, although the wooden roof covering one-third of the cage afforded shelter. The animals lived in small groups, typically one male, two or three females and their infants and juveniles. The animals could see grass and trees beyond the cages, and this fact coupled with their exposure to natural temperature, winds, etc., and group living, served to simulate conditions in the wild, while the dimensions of the cage both vertical and horizontal afforded considerable space for movement.

The Setting - Primate Centers in the United States: In all four primate centers the animals observed lived in individual cages, aligned in rows, facing other cages. At the front of each cage was a food hopper and drinking apparatus. The floors of the cages were grid work, and the cage dimensions for small macaques did not exceed 27" deep x 18" wide x 24" high, and for baboons, 35" wide x 35" deep x 48" or 54" high. A third cage size used for large macaques or small baboons was 30" deep x 27" wide x 30" high. Because of the size of the cages, and the isolation, no interactions pertinent to the study could be made. While the cage rows were outdoors at Delta, they were under a sun-rain shade, enclosed within a screened porch. Thus, the animals were partially protected from sun and rain.

Control of Behavior - Tigoni: No attempt was made to control behavior; no experiments were introduced. The purpose of the observations was to ascertain how the hand in these monkeys is used in ordinary circumstances in captivity. A certain amount of interaction took place between the animals and myself which included watching, grooming, touching and threatening, but captivity imposes a new environment which includes daily association with man.

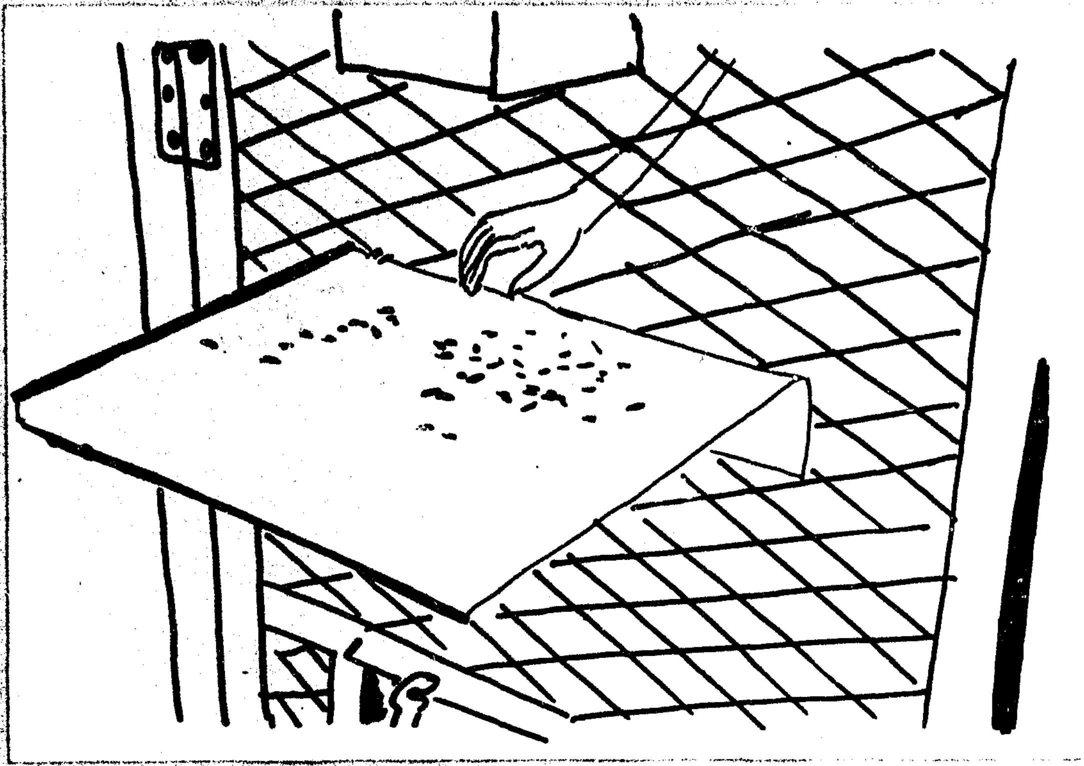
The monkeys were not presented with artificial objects and problems designed to elicit their repertoire of manipulation. Instead, the manner in which food is prepared for eating and conveyed to the mouth was taken as the primary index of the use of the hand. The foods were placed on the concrete floor of the cages.

Some of the foods comprising the diet of the captive animals are not readily available in the wild. Haddow (1952), Booth (1962), Hall (1966), and Struhsaker (1967) report however, that *C.ascanius*, *C.neglectus*, *C.mitis*, *E.patas* and *C.aethiops* raid cultivated fields for crops, many of which were fed at the Centre (granadilla - *Passiflora cere*; sweet potato - *Solanum tuberosum*; and maize - *Zea mays*). Furthermore, it is less likely that behavioral adjustments would result from the introduction of these foods than from the introduction of such objects as blocks, balls, etc.

Control of Behavior - Primate Centers in the United States: The diet at the primate centers is principally artificial "monkey chow" - a nutritive composite fed in compressed chunks approximately 1 and 1/2 inches long, and 1/2 inch wide, with fruits and vegetables served as complementary items (Holloman). The chow is placed in self-feeding hoppers.

As neither the diet nor the manner of feeding elicited the normal repertoire of hand movements, feeding experiments were conducted. A 10" x 12" aluminum tray was constructed with prongs on the long side by which the tray could be affixed to the cage front. The normal feeding apparatus of the cage being removed, a gap in the cage allowed the animal access to the tray with one hand only (Plate I). He

Plate I. Feeding Tray Experiment: Delta



frequently was in an awkward position due to the size of the cage (Holloman) or the fact that the foot-holds were the structural ledges of the cage and one **hand** was needed for balance (Delta). Although the data from these experiments are included, they are used only as comparative material, and are intended to express a tendency. I believe that the lack of free mobility in gaining access to the experimental food detracts from the validity of the frequency counts of manipulative acts in *Macaca* and *Papio*.

The Food Items - Tigoni: Observations were made of the manner in which ten types of foods were prepared for eating and carried to the mouth. The food items were: greens, carrots (*Daucus carota*), white and sweet potato (*Solanum tuberosum*), maize (*Zea mays*), yellow-skinned bananas, mango (*Mangifera*), grain (oats, *Avena sativa*), pineapple (*Ananas comosus*), chow-chows (*Pachystela brevipes*) and granadilla (passion-fruit, *Passiflora cere*). Each of these foods presented some problem to the animal. The general problem was to uncover the edible part of the food, and to convey it to the mouth. Specific problems resulted from variations in size, shape, length and the nature of the covering.

The manner in which the animal resolved the problem a particular food presented was taken as a measure of the manipulative potential of the hand.

The primary problem presented by pineapple and chow-chow (both of which were fed in lengthwise slices), carrots and potatoes, is their size. Granadilla, mango and banana have shells or skins, and these had to be broken or peeled. Lettuce and greens are limp and were awkward to handle. Maize and grain presented the most formidable problems, the former because strength was required both to remove the husk and support the ear, and the latter, because its small size (each kernel approximately 1 cm. long), oval shape and smooth husk necessitated the finest control.

The Experimental Food Item - Primate Centers in the United States: Oats was chosen as the experimental food for primate centers serving monkey chow only. At Tigoni I had found that grain was the best discriminant of fine manipulation, and would register a species' maximum ability. It is convenient to use as an experimental food, being inexpensive and easily transported, and is readily accepted and therefore probably palatable to various species of monkey. It is nutritive, and proposes no digestive difficulties as would fresh greens, etc.

The animals were first exposed to the experimenter, to insure against novelty. The subject was then presented handfuls of the grain because as the animals are fed principally on monkey chow, the food being novel in taste is seized in fistfuls, skewing the results of the test. It was found that if the animal was permitted great quantitities, he became inured to the food, and then neither hunger nor taste motivated him to grab it. At Holloman, where fruits such as apples and bananas constitute a part of the daily diet, it was felt that these items would best serve as the experimental food, because the animal was accustomed to them, and when cut into bits 1-2 cm. long, they offered the same difficulties as grain, being smooth or even slippery, and quite small.

The Hand Positions: Observations were made for several days in order to see how the hand was used. Five primary grips were isolated. These may be seen as a continuum from non-opposed to opposed grips, depending on the movement of the thumb. In the description of these grips, the digits are numbered one through five, beginning with the thumb, and are abbreviated d1 etc. These grips are ordered from those used where fine control is required (one grip opposed and one non-opposed), to those where strength is sought (two opposed and one non-opposed) (Plate II).

Single-Hand Positions:

Refined Opposition (RO): The thumb is flexed, abducted and medially rotated, so that the palmar surface of the distal phalanx can come into contact with the palmar pad of the distal phalanx of d2. The second digit and thumb may contact each other in a forceps grip (Wood-Jones, 1920) which Kaplan (1953) has called "closed elongate" opposition, in which both phalanges of both digits are fully extended, and the pollical metacarpal flexed. The second digit and thumb may also contact each other in a circle grip, Kaplan's "closed round," in which the phalanges of both digits are fully flexed, as is the pollical metacarpal.

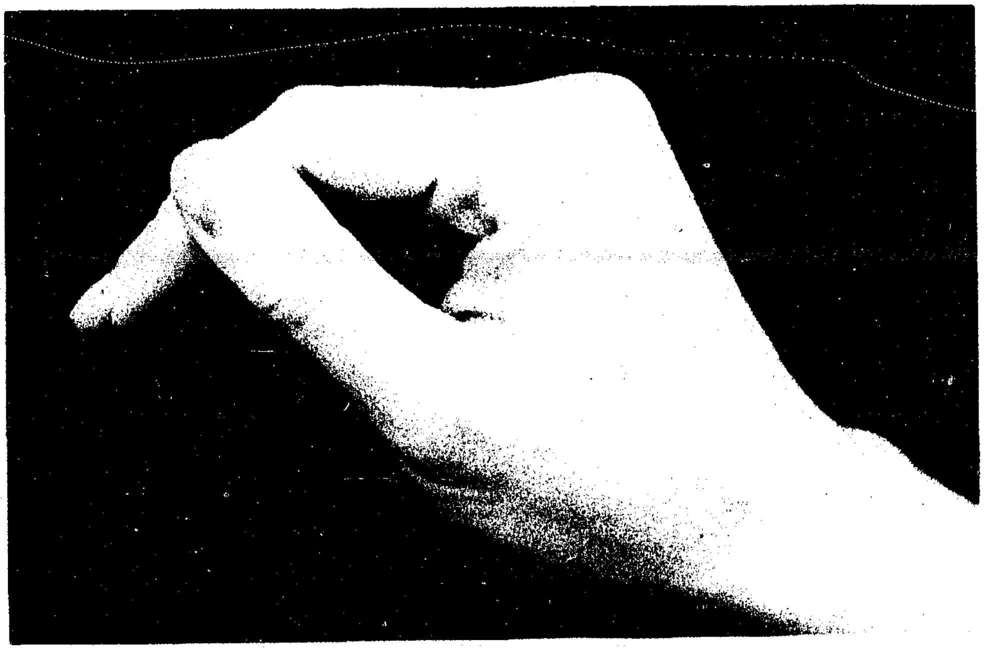
The RO is the position the human hand assumes when performing fine tasks such as threading a needle or writing, or tool-making, in which precision is required. The RO, although subsuming precision, is NOT identical to Napier's concept "precision grip" (1961, 1966), since he does not distinguish between opposition and precision. In his precision grip, "The fingers are slightly flexed at the metacarpophalangeal joint and interphalangeal joints. The thumb is abducted, flexed and medially rotated (opposed position)" (1966, p. 26). His figure illustrating the precision grip (1966, p. 25, 12 b), shows a hand holding a round object so that the pad of the thumb is equidistant from the other digits. While this is an opposed grip, it can be accomplished without fine control or precision. According to Napier, there is a progression of hand position from convergent (tarsier) to prehensile (Callithrix) to pseudo-opposable (Cebus) to opposable (O.W. monkeys, man) (Napier, 1961, 1967). Each successive stage has as its correlate increased control of the hand in manipulation. Precision (Refined Opposition) reflects a refinement in the efficiency of opposition.

Quasi-Opposition (QO): The pulp surface of the thumb is pressed against the side of the index finger, anywhere from just proximal to the head of the first phalanx to just proximal to the tip of the distal phalanx. Although it is frequently the nail surface of the distal phalanx of the thumb that is pressed against the index finger, no distinction in terminology has been made. This is a non-opposed grip, though quite similar to the RO in that as the first digit is pressed against the side of d2, rotation of the metacarpal and proximal phalanx occurs, along with contractions of the flexors, which in this position stabilize the first digit. Some adduction, probably of the oblique rather than the transverse assists the flexor brevis in stabilizing the digit. Abduction is very slight, if at all, and primarily of the brevis, as the thumb contacts the index on the head of the 1st phalanx. The more distal on d2 the grip is assumed, the greater the role of the abductors.

The structure of the hands of the Cercopithecus species studied inclines those animals to use this position most frequently. Used where human beings would use the RO, it does not permit equally fine manipulation of objects. Whereas the contact between the pulps or tips of d1-d2 allows both digits to move, the pressure exerted on d2 by d1 in the QO curtails the flexibility of d2. When a pencil is held in the hand in the RO grip without aid of d3 as in

Plate II. Hand Positions

Refined Opposition



Quasi-Opposition

normal writing, it can be seen that d2 is equally involved with d1 in manipulating the object. Altering the grip to the QO demonstrates that either d1 alone is moving the object, or the wrist is required to move the object as held in a vise, with consequent decrease in dexterity.

The remaining three grips were used primarily where strength was necessary.

CUP: In the CUP grasp, the palmar surface of d1 presses the object equally against the palmar surfaces of d2-d5, in order to secure it as in holding a ball or apple. As mentioned above, Napier considers this a precision grip (1966 and personal communication), but its function is strength more than control, and seems best considered separately. The thumb is opposed to the other digits which are flexed so that they arch.

FIST: In this position, and the one following, the work is done by d2-d5 and the thumb is virtually or entirely functionless. In the FIST, d2-d5 surround the object, and serve to secure it. The thumb merely closes over the digits, so that its distal palmar surface touches the dorsum of the middle phalanges of d3 or d4 or both. The thumb is abducted, flexed and medially rotated, and to this extent is opposed, but its distal phalanx cannot contact the volar pads of the other digits. It is a form of what Napier has termed the "power grip" (1966).

Plate II. Hand Positions

FIST

Non-Opposed

Table 1

Summary of Movement of the Thumb Relative to the Second Digit

	Refined Opposition	Quasi-Opposition	CUP	Non-Opposed
Abducted	X		X	
Flexed	X	X	X	
Medially Rotated	X	X	X	
Adducted		X		X
Extended				X
Relation to d2	Tip to Tip	Contacts Side	Opposes all Digits	Lies Alongside d2

Non-Opposed (N-O): The N-O is similar to the FIST because d2-d5 secure the object against the palm of the hand, however, the thumb is entirely functionless in this grip. It is fully extended and adducted, so that the medial border of its distal phalanx is held alongside the lateral border of the proximal phalanx of the index.

Double Hand Positions:

COB: The COB resembles the CUP, but differs in that it is only assumed in double-hand usage, and in that the curvature of the digits is greater. It is the tips of d2-d5 that maintain the object against the palmar surface of the distal phalanx of d1.

Double QO, Double CUP, Double FIST: The QO, CUP and FIST also exist as double QO, etc., since the animal frequently picks up an object with both hands in the same position. Any combination of grips, however, may also occur, thus QO left - N-O right; CUP right - FIST left, etc.

Photography

Both movie and still photographs were taken to verify observations and to analyze motion which the eye can barely perceive. Movies were taken with an 8 mm camera at 16 frames per second. A single lens reflex was used for the stills.

Anatomical Data

Measurements

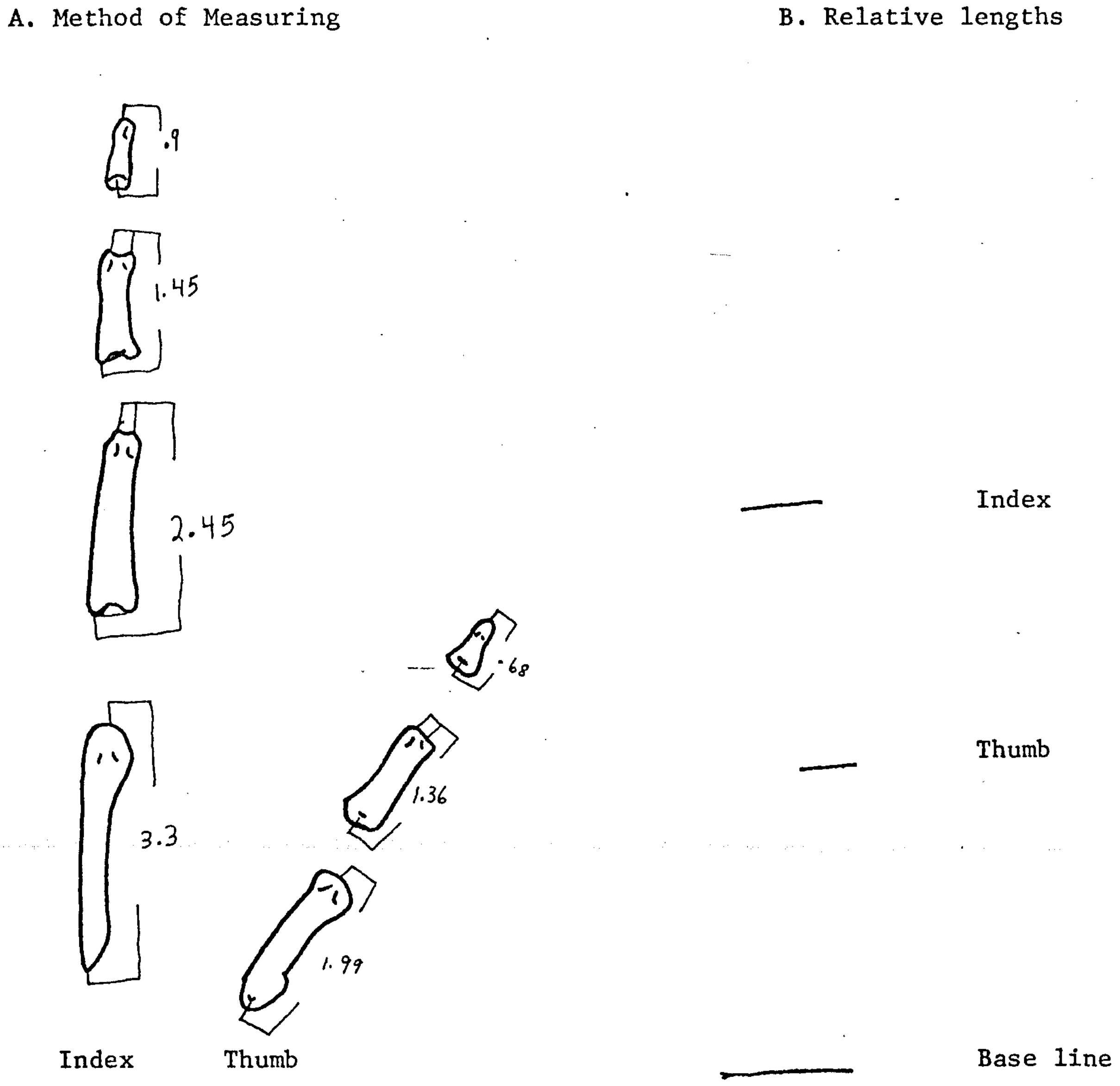
The motive for using an index derived from the length of the thumb divided by the length of the second digit times 100, is that it reflects the functional unit of opposition more closely than does the "Pollicial Index" (Ashley-Montagu, 1931), which measures the thumb length against that of the third digit. While the Pollicial Index is the one used by Schultz (1926) and others (e.g., Krogman, 1942), the advantage of the functional index described has been recognized by Napier (1967) who refers to it as the "Opposability Index" which term is used throughout this thesis.

Measurements were made on disarticulated specimens available as part of the permanent collection at Tigoni, and hands in the United States which had been partially dissected but were still articulated. At Tigoni, only adults of the species were chosen. Separate readings standardized to the longest length were made with vernier calipers on metacarpals I and II and on each phalanx of the pollex and index. No allowances were made for articular cartilage, which introduces a slight error of comparability of separate dry bones and articulated specimens. The method for measurements made on articulated hands was found to be identical to the technique employed by Napier (1967),

Figure 1.

THE RATIO OF THE LENGTH OF THE THUMB TO THE LENGTH OF THE INDEX FINGER:

OPPOSABILITY INDEX



A. Method of Measuring

B. Relative lengths

C.neglectus MHS 19

that is, from the base of the thenar metacarpal on the radial aspect to the tip of the terminal phalanx, and from the base of the indical metacarpal to the tip of its terminal phalanx. As the method was the same, a means exists of comparing measurements by different investigators. Although a convenient method for measuring, I believe it is less reliable or accurate than measuring disarticulated, individual bones, which can be firmly held totally within the arms of the caliper, and gripped in a standard fashion, that is, always from the longest point to the longest point. Measurements of articulated, ligamentous specimens tend to be subject to the variations of drying of soft tissues and difficulty in applying the calipers and thus getting consistent readings.

Dissections

Dissections of the antebrachial and pollical muscles involved in moving the thumb were made of fresh, frozen (and very occasionally) formalin fixed adult or subadult specimens. Table 2 shows the number of each species, age, and provenience. The purpose of the dissections was to attempt to relate the morphology of the hand with its observed behavior. As the sample of animals dissected at Tigoni was donated by trappers and farmers and the Kabate veterinary school, they represent a cross section for their species, and the sample is large enough to encompass variation and show tendency for the species, though not sufficient to show sexual dimorphism if any. This study was dependent on donations, and few specimens of C.neglectus and Colobus abyssinicus were available, while there were none for C.ascanius.

The specimens from the United States Primate Centers were not purposefully sacrificed, but were donated by other researchers. At the Regional Primate Center of the University of Washington, I examined a collection of M.mulatta fetuses preserved in gelatin and stained with Alizarin.

Radiology

At the University of Washington, I examined a series of radiographs of M.mulatta. Further films of Papio doguera, C.diana and M.mulatta were made with a Pickering machine, 36" from the hand, set at MA 15 and KV 42, and exposed for one second. The assistance of a radiologist permitted taking x-ray movies of a M.mulatta female manipulating food items. The x-ray material was used in studying the critical relationship between the thumb and d2 in the position of the hand at rest, that is, where "...the forearm is somewhat pronated; the wrist flexed; the palm of the hand hollowed; the digits bent in toward the palm...the thumb held midway between flexion and extension..." (Wood-Jones, 1920, p. 115).

The concept "Passive Opposition" has been developed

Table 2

The Specimens and their Provenience

Species	Sex	Tigoni	Holloman	Sterling Forest	Delta	Total
C.aethiops	M	4			1	9
	F	3			1	
C.neglectus	M	2				3
	F	1				
C.ascanius	M F					
C.mitis						
Sykes	M	3				7
	F	2				
Blues	M	2				
	F					
E.patas	M	2				6
	F	2			2	
Colobus abyssin.	M	1				3
	F	2				
M.mulatta	M		2		1	8
	F		3		2	
P.doguera	M			2		5
	F			1	2	
Pan troglodytes	M		2			4
	F		1		1	
Hylobates lar	M			1	1	2
	F					
Gorilla	M					
	F		1 (infant)			1
					TOTAL	48

by Napier and Davis (1959) to reflect the phylogenetic differences between man and the non-human primates. The term refers to the position of the thumb relative to the other digits when the hand is in the position of rest. As defined by Napier and Davis (1959) for man, the thumb lies on its radial border rotated on its own axis, so that the palmar pad of the distal phalanx can easily contact the palmar pads of the other digits. While an angle has been found for estimating the degree of Passive Opposition in Cercopithecidae, as it is taken between the articular surface of the trapezium and the dorsum of the capitate (Napier and Davis, 1959), this angle does not reflect functional differences. This difficulty occurs because the dorsum of the capitate is not a plane, but part of an arc, and because the relationship of the thumb to d3 is the same as its relationship to d4 or d5. The relationship of the thumb to d2 is the only critical one, because it is this unique configuration which is the unit of fine manipulation.

An evaluation of Passive Opposition and its dependence on osteological relationships was made with x-ray data and freshly dissected specimens. These relationships include the articulation of those carpals between the radius and metacarpal I and II. They equally concern the articulation of metacarpal I to the trapezium.

With the arm held resting on its elbow and secured in the position of rest, the relationship of the head of the metacarpal of the thumb to the head of the metacarpals of the other digits gives an appreciation of the amount of movement required to position the thumb for precision use. Schultz (1926), notes this posture from a different view, but with the hand still in the position of rest. Looking at the hand towards the finger tips, the amount of rotation of the metacarpals and phalanges of the thumb relative to the plane of the other digits can be observed (see Fig. 3).

CHAPTER IV. THE DATA

Ecological Data: Habitat and Diet

Cercopithecus

The ecological literature of each of the species was examined to evaluate possible reasons for differences in manipulative performance.

All four species of Cercopithecus studied are arboreal (Haddow, 1952; Struhsaker, 1967; Tappen, 1960). The degree to which the tree environment is exclusively exploited varies, however, with a gradient running from C.ascanius to C.mitis, to C.neglectus and to C.aethiops, the latter being readily found on the ground (Struhsaker, 1967). The habitats of these species overlap (Haddow, 1952; Struhsaker, 1967; Tappen, 1960), and three of the four species can be found in the same forest zone (Tables 4 and 6).

Cercopithecus ascanius is found in northern and eastern parts of the Congo, as well as southern Uganda and western Kenya (Haddow, 1952; Tappen, 1960). It is reported to be primarily a rain forest (both lowland and upland) and gallery forest species (Haddow, 1952). C.ascanius is absent from savanna, requiring zones of thicker foliage. Its actual habitat is a stand of tall trees, so that individuals may be found in such isolated groves as plantations though no actual forest is nearby (Haddow, 1952). Haddow reports that in such areas, C.ascanius subsists mostly on raided crops.

In the gallery forests, C.ascanius is found both in old and second growth areas, but is relatively scarce in ancient high canopy growth of the interior of such forests. When it does occur in the interior, it is because small streams or marsh rivers quite similar in vegetation to the forest edge are found (Haddow, 1952).

According to Haddow (1952), life activities are conducted in the lower levels of the canopy, except when a crop of fruit is available in the higher regions. For the same reason, they can be found quite as infrequently on the forest floor (Haddow, 1952). Tappen (1960) feels that this observation may be restricted to Bwamba forest, as he has observed C.ascanius at all levels of the forest.

Their diet is varied, consisting of tree leaves, green shoots, tree flowers, fruits - especially figs when they are available - and cultivated crops, particularly maize, banana, pineapple, sweet potato, passion fruit, beans and finger millet (Haddow, 1952). Knowledge of the foods enumerated in order of frequency of eating, was accumulated by Haddow not only from field observations, but by analysis of the stomach contents of 100 wild specimens (Haddow, 1952). Hard kernels or seeds are not eaten - the fruit being exploited for its pulp. Many of the fruits are surrounded

Table 3

Time Spent on Ground:

The Author's Arbitrary Scale 1-10

Rank Order	
C.ascanius	.5 - 1
C.mitis	2
C.neglectus	3
C.aethiops	5 - 7
M.mulatta	5 - 7
E.patas	9
P.doguera	9

Table 4

Range Overlap of Species Studied

```
    C.        C.       C.     C.        P.      E.      M.
neglectus  ascanius  mitis  aethiops  doguera  patas  mulatta

   /----------------------------/
             /---------------------------/
                                /----------------/
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with a heavy covering. Haddow never witnessed any C.ascanius, or any other Cercopithecus eating birds or bird eggs, or other vertebrates (Table 5).

C.mitis' habitat is quite similar to that of C.ascanius, except that it may range a few thousand feet higher in altitude (Tappen, 1960). C.mitis are found primarily in East Africa, from Central Ethiopia to parts of Zambia, although they are known in northwestern Angola as well. They are the only Cercopithecus species other than C.aethiops, according to Tappen's study, that are found in the south of the continent. Like C.ascanius, they frequent wet forest, both montane and gallery, though they have been observed by Schouteden (1947) in savanna woodland, a fact which Tappen (1960) believes warrants further examination.

The C.mitis comprise two races, identified as such by Cynthia Booth (1962). The Blues (C.mitis stuhlmanni) are more restricted to eastern Africa and parts of Congo (Tappen, 1960; Hill, 1966) into southern Ethiopia (Starck and Frick, 1958). According to Booth (1962) the range of the Blue monkey is separated from that of the Sykes in Kenya by the Rift valley, the Blues inhabiting the western portion of the valley. Both races occupy broad-leafed forests and bamboo groves. C. Booth has found natural hybrids of these races in the wild, and has bred hybrids at the Tigoni Primate Centre (1962). Like C.ascanius, C.mitis is primarily an eater of leaves, shoots and fruits (Table 5). Booth has noted that *C.mitis*, like *C.ascanius*, raids cultivated fields for the maize, potatoes, and beans (Booth, 1962).

C.neglectus, commonly called the de Brazza monkey, is known from the northeastern part of the Congo basin, west to Gaboon and Spanish Guinea and Southern Cameroons, and isolated patches in the east (Tappen, 1960), as noted by Haddow in Uganda (1952), Booth in Kenya (1962), and documented for Ethiopia (Hill, 1966). Although an arboreal, forest species preferring riverside forest and swamp land, it is now known not to be exclusively so, contrary to Haddow (1952). *C.neglectus* is known to use the ground and to traverse the forest floor (Booth, personal communication). It has been observed to use the forest floor regularly when escaping from danger (Tappen, 1960). In the exploitation of the ground it is rather different from the other Cercopithecus species just mentioned. As shown in Table 5, their diet includes leaves, and fruits principally, but they are known to eat insects and raid cultivated crops (Booth, personal communication).

C.aethiops is the best known species of Cercopithecus. They are widespread over most of the African continent, found from Senegal to Ethiopia, from Sudan to the tip of South Africa (Tappen, 1960). Although the vervet has been found in gallery forest in Ethiopia (Starck and Frick, 1958), it typically lives in a drier habitat than do the other species of Cercopithecus. This species prefers the wooded areas marginal to the forest, and true savanna (Starck and Frick, 1958; Hall, 1965; Hall and Gartlan, 1965; Struhsaker, 1967), that is, zones with grasses as the main ground cover, and flat topped trees, like the acacia (Moreau, 1952). However, "It is rare or absent where arid conditions prevail," or in rain forest (Tappen, 1960).

While Haddow (1952) found that the *C.ascanius* does not drink water, Struhsaker noted that the group of *C. aethiops* he observed in the Amboseli, "...visited a water hole on the average of about once every two days" (Struhsaker, 1967, p. 996), an observation confirmed by Hall (1965), and Hall and Gartlan (1965).

In savanna, *C.aethiops* is primarily dependent on species of the Acacia - the fever tree - which affords sleeping places, food and refuge from predators (Struhsaker, 1967). While the more arboreal species like *C.ascanius* eat the gum of this species only (Haddow, 1952), *C.aethiops* eats the beans, leaves and seeds (Table 5). Like other savanna, or part-time savanna dwellers, they exploit most, if not all, the resources available to them. *C.aethiops* monkeys are considered omnivores (Booth, 1962), and have been observed by Struhsaker (1967) to enjoy birds, poultry eggs (Maberly, 1963), hares (Booth, 1962) as well as the more usual insects

Table 5

Diet of the Species Studied as Recorded in Field Reports

	C. ascanius	C. mitis	C. neglectus	C. aethiops	E. patas	P. doguera	M. mulatta
Tree							
Leaf	x	x	x	x		x	x
Leaf bud							
Flower	x						
Roots							
Cultivated Crops	x	x	x	x	x	x	x
Fruits	x	x	x	x	x	x	x
Grasses				x	x	x	
Seeds	No			x	x	x	
Berries				x	x	x	
Meat							
Vert.				x	x	x	
Invert.	x	x	x	x	x	x	x
Pods					x	x	
Beans				x			

Note:-- Field reports as follows:
C.ascanius - Haddow, 1952; C.mitis - Booth, 1962; C.neglectus - Booth, p.c.; C.aethiops - Struhsaker, 1967; E.patas - Hall, 1966; P.doguera - Devore & Hall, 1965, Tappen, 1960, Devore & Washburn, 1963; M.mulatta - Southwick, 1966; Neville, 1968.

(termites, ants, beetles) (Hall, 1965), eaten by other monkeys (Haddow, 1952). Mature fruits and berries are preferred when available, but the base of grasses and stems, leaf buds, leaves and seeds are more frequent in their diet (Struhsaker, 1967).

C.aethiops overlaps with other *Cercopithecus* species as in the Kibwezi river, Kenya, where they are found with *C.mitis* (Booth, 1962), or in the Semliki valley, western Uganda, where they have been seen with *C.ascanius* (Haddow, 1952) or Namah river in northeastern Uganda with *C.neglectus* (Struhsaker, 1967). Where there is overlap, *C.aethiops* generally occupies the niche of sparser vegetation, while the other species are in the areas of denser vegetation as noted above. Competition does exist with the truly terrestrial species of Cercopithecidae, the *Papio* spp. and *E.patas* (Hall, 1965) (Table 4). Booth (personal communication) suggests that the abundance of *C.aethiops* is a function of its flexibility: this species is able to cope with savanna, which implies utilization of ground resources, and to live in forest as well. Struhsaker notes (1967) that trees remain important to *C.aethiops* even in savanna not only because they are a prime source of food, but because "...extreme arboreal agility [is] their major defense against diurnal predators" (p. 903).

The *Papio* - *C.aethiops* relationship observed by

Table 6

Habitat of the Species Studied as Reported in the Literature

	C. ascanius	C. mitis	C. neglectus	C. aethiops	E. patas	P. doguera	M. mulatta
Tropical Forest	x		x				
Gallery Forest	x	x	x	x (Ethiopa)			
Montane Forest	x	x	x			x	
Sparser Forest		x	x	x			x
Woodland		x (?)		x	x	x	x
Swamp			x				
Savanna				x	x	x	

Note:-- Reported in the literature by:

Haddow, 1952 - C.ascanius
Haddow, 1952; Booth, 1962; Tappen, 1960 - C.mitis
Booth, 1962; Hill, 1966; Haddow, 1952 - C.neglectus
Struhsaker, 1967; Hall & Gartlan, 1965 - C.aethiops
Hall, 1966 - E.patas
Devore and Hall, 1965; Devore and Washburn, 1963 - P.doguera
Southwick, 1966 - M.mulatta

Struhsaker (Table 4) was as much one of predation as mutualism. This was confirmed by Devore and Washburn (1963), although not noted by Hall (1965). While they utilize each others warning calls of the presence of jackal, eagle and other predators, baboons have been observed to eat verets, especially the immature (Struhsaker, 1967).

Erythrocebus Patas

Hall (1965) found the E.patas monkey living not only with baboons, but with vervets as well, and while yielding ground to the baboons, they would tease the vervets by running up to them, making noises, but never really attempting to attack. Vervets compete with E.patas as they do with baboons, but the competition with baboons is limited since the smaller vervets lack the strength to take certain foods, such as some of the grass plants (Struhsaker, 1967). Competition with E.patas is limited since the vervets use trees more.

E.patas, whose generic name has shifted from Erythrocebus to Cercopithecus and back again since 1907, are the most terrestrial of the Cercopithecinae and/or their relatives. According to Hall (1966) they may be even more savanna-adapted than baboons, both in morphology and behavior. As shown in Table 6, they occupy three types of habitat: (1) woodland steppe, (2) tall grass, savanna and (3) woodlands of relatively moist type with dense tall grass (Hall, 1966). They are known mostly from areas north of the equator, from Senegal in the west to Sudan in the east; their northern limit is the edge of the sahara. They are also found in southern Uganda and from western Kenya to western Tanzania. Their southern limit is the forest belt of southern and western Cameroon and Congo (Hall, 1966).

Like *C.ascanius*, and therefore, contrasting with the vervets and baboons, *E.patas* have been rarely observed to drink. When they have been seen to do so, it was for periods of very short duration. These animals are "manual grazers" (Napier, 1967), walking and eating in the same movement, as do baboons (Hall, 1965). As shown in Table 5, their diet is comprised almost entirely of grasses, berries, fruits, beans and seeds. The tamarind is the most important source of food, offering pods, fruit and pulp. Their diet is supplemented by occasional mushrooms, ants and grasshoppers and small lizards; a diet very like that of the baboon. Hall feels that in spite of the similarity, there are sufficient foods eaten by one species and not the other to restrict competition and permit them to occupy the same area. Like the other species discussed, *E.patas* will raid cultivated fields, pilfering millet, cassava, banana and even cotton (Hall, 1965).

Papio doguera

Although no Papio doguera were captive at Tigoni, five individuals of doguera (anubis) were studied in the United States in order to gather data for comparison with the terrestrial Cercopithecus species and the closely related E.patas. The olive baboon lives in the Kenya highlands, many parts of Uganda, the eastern and northern parts of the Congo (Tappen, 1960), and if, as Devore and Hall have suggested, P.ursinus or comatus is to be considered a racial variant, the range continues to South Africa (Devore and Washburn, 1963; Devore and Hall, 1965).

Their habitat is savanna, ranging from the arid to the woodland phase (Tables 4 and 6), although they have occasionally been seen along the margin of the forest (Devore and Washburn, 1963) or in the forest (Rowell, 1966). While a terrestrial animal, the baboon uses tall trees, such as fig and acacia for sleeping places and refuge from predators (Devore and Hall, 1965). Although taking whatever food the trees may offer, the savanna baboon is a manual grazer (Napier, 1967). Grasses, especially the stems, form a major part of the bulk of the diet (Table 5), amounting at least in the dry season, to nearly 90% of foods consumed (Devore and Washburn, 1963; Devore and Hall, 1965). Vegetable foods are primarily taken from the ground, that is, roots, tubers, seeds and the grasses (Devore and Washburn, 1963; Tappen, 1960). However, fruits on shrubs and trees, particularly the fig, constitute an important part of the diet when these are available (Devore and Washburn, 1963). Vegetable proteins are augmented by the capture of vertebrate and invertebrate animals. Insects are eaten as are reptiles and mammals (Devore and Washburn, 1963; Devore and Hall, 1965). Devore recorded six such predatory episodes in 10 months, the prey including hares, Thomson's gazelle, and vervets (Devore and Hall, 1965).

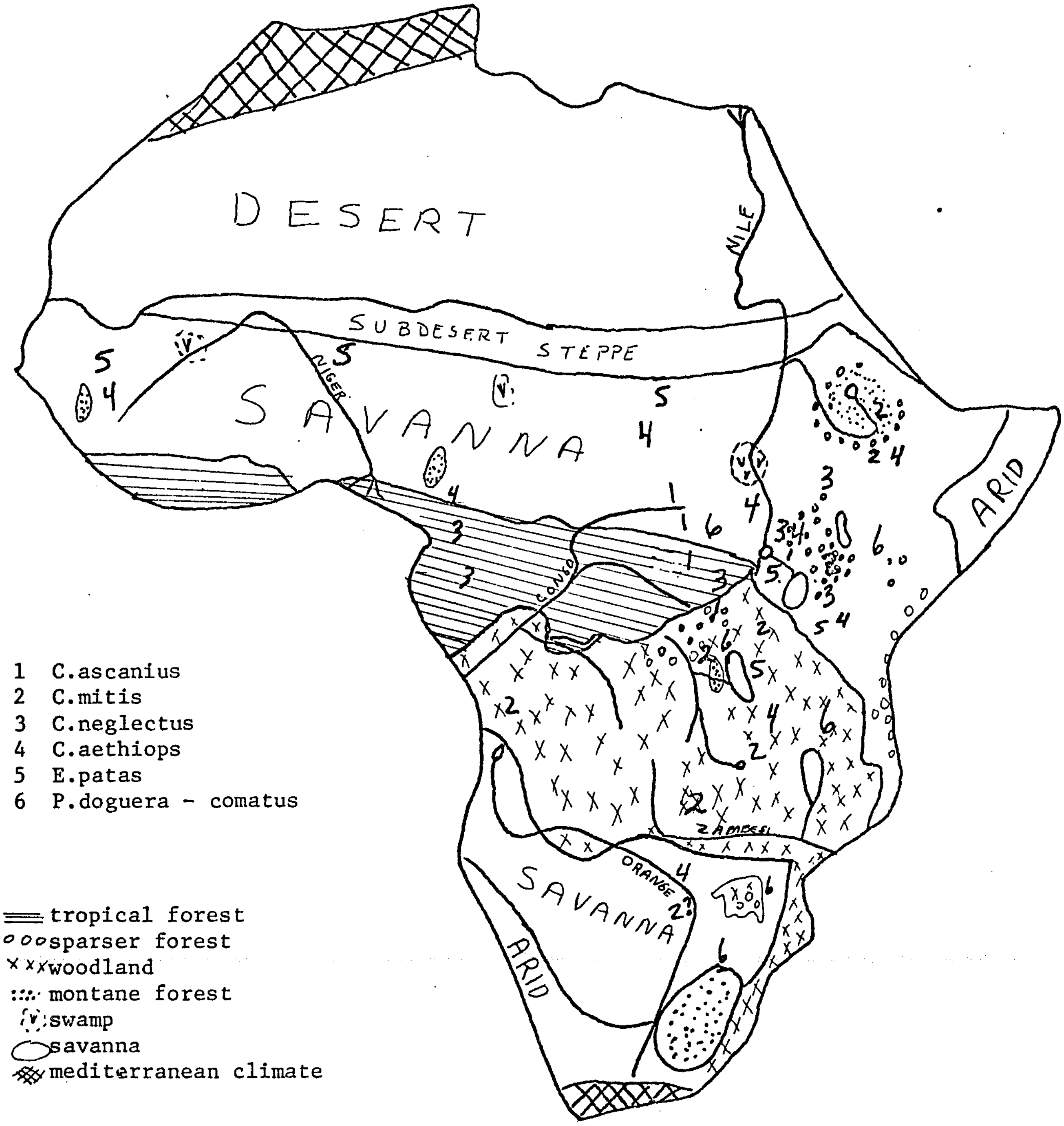
Macaca Mulatta

Another genus and species of monkey, *M. mulatta*, was studied in the United States not only because of its exuberant availability, but because it occupies the same position in Asia that the vervet has in Africa, that is, it is equally at home in the trees or on the ground (Southwick and Siddiqi, 1966; Neville, 1968).

In spite of its great popularity as a research animal, the earliest authoritative study of the rhesus in the wild was made by Southwick (Altmann, 1962). Since then, studies have been made by Southwick, Siddiqi, *et al.*, 1961, 1965, 1966, and Neville (1968).

The range of the rhesus is from Kashmir to Assam, to Burma and Thailand and north to China. In India they are found as far south as the Godaveri river and as far west as

DISTRIBUTION OF SPECIES STUDIED



1 C.ascanius
2 C.mitis
3 C.neglectus
4 C.aethiops
5 E.patas
6 P.doguera - comatus

═ tropical forest
ooo sparser forest
xxx woodland
∴ montane forest
(v) swamp
⬭ savanna
▦ mediterranean climate

zones compiled from Moreau,1952 and
Cooke,1966

the Gujerat river (Pockock, 1932; Southwick, et al., 1965). The rhesus are generally thrown into greater contact with man than are the African monkeys. Neville (1968) remarks, for example, that in his study area in the foothills of the Himalayas, there are only two forest areas left. The rhesus must live from donations made to them, which, although they are considered quasi-sacred by Buddhists and Hindus (Carpenter, 1940) are becoming less frequent (Neville, 1968). They therefore must raid from field or town, procuring rice, maize, potatoes and sugar-cane (Southwick and Siddiqi, 1966; Neville, 1968) (Table 5). In the forests the rhesus forage on the ground and in the trees, their diet being principally leaves and fruit (Napier, 1967) but including roots and insects (Southwick, et al., 1965).

Behavioral Data: Observation of Manipulative Behavior

Napier (1962, 1967), stresses the significance of the strata of the forest occupied by a given species, a concept developed in Cain's Manual of Vegetational Analysis (1959). Napier sees the stratum as influencing adaptations in the extremities. He agrees with Avis (1962) that the thickness of tree branches as well as the angle in which they lie relative to the trunk, has been influential in the evolution of the locomotor systems of the various species, and their concomitant behavioral development. Admitting that the distribution and density of foods are involved in stratification, Napier nevertheless places greater emphasis on *getting* to the food than getting the food from its source into the animal's mouth:

> The maximum density of fruit and leaves thus tends to be sited peripherally; in order to reach and feed on the leaves, the animal is forced to move far out from the trunk into a milieu that is largely composed of small flexible branches; in such a setting the suspensory activities of the hands, feet.... are called into play (1967, p. 384).

The *nature* of the food itself, would seem to require morphological adaptations as well. *E.patas*, for example, cannot eat the baobab fruit (Hall, 1966), which has a very hard husk. Baboons do consume them, however, with ease, as *E. patas* simply does not have the requisite strength of hands, jaws and teeth to dismember this fruit. Yet both occupy the same biome and both are digitigrade quadrupeds (Oxnard, 1963; Devore and Hall, 1965; Hall, 1966; Napier, 1967). Quantified analyses of foods and the frequency of their ingestion have been made by Haddow (1952) and Struhsaker (1967) for *C.ascanius* and *C.aethiops* respectively. Similar detailed information does not exist for the other species under consideration. Observational studies and experiments with caged animals give some insight into the *facility* with which certain foods are manipulated, and when the facility of manipulation correlates with the availability of that food in the wild, an adaptive tendency may have been located.

Table 7

An Inventory of the Individual Living Monkeys Studied at Tigoni

Species	Place		Female	Male	Subadult	
	Cage	Row	Adult	Adult		
<u>C.mitis</u>						
Sykes	5	1	Molly	Oliver		
			Chick's ma		Hybrid	
	13	3	fem.1			
	12	3	fem.1	Friar		
	14	3	Ruth	Rufus		
			Naiomi			
			fem.3			
	11	3	fem.1.(bad eye)	Mwangi		
			fem.2.(larger)			
			fem.3			
	16	4		Jeremy	Chico	Chiclet
	4	2			sub	
	20	5				Chickweed
Blues	25	5	Kiki	Poohba		
			Janet			
	6	1	Katisha	Jack #2		
				male		
	5	1		Coco		
<u>C.neglectus</u>						
	15	4	Mu	Tinkler	Eeaw	
			Biddie			
			Buntie			
	10	2	fem.	Mikki		
	24	5	fem.1		sub	
			fem.2 (brok.finger)			
	23	5	Alice	Kara		Bessie
		2	fem.	male		
	31	below	Beatrice	Bishon		
<u>C.aethiops</u>						
	2	1	Diana	Delinquent	Dennis	
			Sukki			
	18	4	Pippa	Tidler		
	17	4	fem.	Mdheroni		
	26	5	fem.younger inf.	Sugari		
			fem.older inf.			
	16	4		Pip		
	4	1			sub	

Table 7 (cont'd.)

Species	Place Cage	Row	Female Adult	Male Adult	Male Subadult	Female Subadult
C.ascanius						
	4	1	fem.			
	3	1	fem.	Bert	Charlie	
E.patas						
	22	5	Yingtong fem. fem.(bitten tail)			
	21	5	Sue-Sue fem. fem.(smaller)			
	27	below			broken 3rd male	bent ear female (smaller)
Colobus abyssinicus						
	28	below	Big girl Bertha	Big Boy Middling		
	29			Pisifu Saki		
	30				Julius Hector	

Observations at Tigoni

Fifty observations per food category per species were made (except for the thumbless Colobus abyssinicus), totaling 1700 observations. Counts were made from as great a proximity to the cage as possible which would not affect the animals. This distance was generally one foot. Only adult or subadult animals were observed to eliminate the factor of motor control. Observation began when food was set before the animal, and terminated when a feeding bout stopped or the animal only picked at the food. Species totals from the individual animals were made per food and scaled to the count per species by proportion.

Table 8 gives the grip frequency counts per food category per species, and Table 9 gives the totals and percentages. The species are listed as a gradient from the arboreal C.ascanius to the terrestrial E.patas.

While the single most favored grasp for all species is clearly the Quasi-Opposed, reaching 30.4% of the total observations, it is notable that the frequency of this grip is lowest in the terrestrial E.patas. Hall and Mayer's experiments with captive E.patas do not confirm this finding (1966). In precision grip tests involving removal of sunflower seeds from strings with different diameters, boards and jars, they found a distinct preference for what is here termed the QO. Unfortunately, the artifical test situation did not include seeds or other food objects of smaller dimensions and different textures. While the QO was represented in the E.patas repertoire at Tigoni, it played a minor role, 4.1% of total observations, as compared to 6.7% for C. ascanius and C.mitis, 6.4% for C.neglectus and 6.3% for C. aethiops.

There is a correlation between frequency of Refined Opposition usage and the exact manner of assuming the Quasi-Opposed. The higher the RO percentage, the more distally the QO is assumed on the second digit. The gradation runs from C.ascanius, who used the RO .1% of the total observations, to E.patas, with 2.1%. In using the QO the C.ascanius contact the pulp of the thumb to the head of the first phalanx of the second digit. C.mitis, with .8% RO usage, generally contact the thumb with any part of the second phalanx of the second digit. C.aethiops, with 1.0% RO usually assume the QO at the head of the second phalanx, and C.neglectus, with 1.2% RO, contact the tip of the thumb to the distal phalanx of d2, below the base of the phalanx. When E.patas assume the QO, the tip of the thumb is pressed against the last phalanx, quite close to the tip. This correspondence between frequency of RO use and manner of assuming QO suggest an anatomical basis for the facility of RO use. Given that the foods the different species were manipulating were the same, the emphatic differences in frequency of RO use reflect on an interrelationship between environment, resources and structure.

The QO was invariably used where as fine a grip as possible was required to manipulate the small particles, so it was most frequently observed in conveying grain, and small bits of broken carrots, bananas, etc. Lettuce and greens, by their texture, thickness and shape required as secure a grip as possible, and therefore likewise elicited the QO. When the RO was employed, it was on the same foods, thus for the same purpose, i.e., precision use as just described for the QO. This suggests that if the RO were anatomically as readily assumed, it would be used whenever fine manipulation is required.

Of the remaining single hand grasps, the CUP was used in 20.2% of the observations, the N-O 15.%, and the FIST only 4.35%. The CUP was selected for foods spherical in shape, like the granadilla and mango. Like the Quasi-Opposed, it was also used when the foods had been broken, bitten or cut into smaller pieces. As it is an opposed grip, the thumb is in a position to exert great force securing an object against the digits.

The QO is easier to assume than the RO in that the intrinsic muscles of the thumb stabilize the metacarpal, and acting through the dorsal expansion operate over the proximal phalanx as well. In the RO by contrast, there is greater

Table 8

Counts of Grip Frequency Per Food* Category

Species	RO	QO	CP	F	N-O	COB	N-O	QO	CP	F
Ascanius										
grain	1	47	1	1	-	-	-	-	-	-
pas-man	1	6	26	-	4	-	-	-	-	13
pot		11	6	-	21	3	4	-	5	-
ban	-	8	19	2	11	5	3	-	2	-
chow	-	6	9	-	11	21	2	-	1	-
carr	-	7	14	1	24	1	2	-	1	-
lett	-	30	-	3	17	-	-	-	-	-
TOTAL	2	115	75	7	88	30	11	-	9	13
Mitis										
grain	11	38	1	-	-	-	-	-	-	-
pas-man	-	8	35	-	3	-	-	2	2	-
pot	-	21	13	-	5	4	4	-	3	-
ban	1	15	16	2	10	1	1	1	3	-
chow	-	16	11	-	9	18	1	-	5	-
carr	-	11	6	1	13	6	2	1	10	-
lett	2	16	2	16	4	-	-	-	-	-
TOTAL	14	115	84	29	44	29	8	4	23	-
Neglectus										
grain	17	28	5	-	-	-	-	-	-	-
pas-man	1	5	28	-	-	-	1	-	15	-
pot	-	13	12	-	14	3	5	-	3	-
ban	1	17	19	-	8	3	1	1	-	-
chow	-	14	7	2	12	13	1	1	-	-
carr	-	11	8	-	17	8	3	1	2	-
lett	3	22	6	6	13	-	-	-	-	-
TOTAL	22	110	85	8	64	27	11	3	20	-
Aethiops										
grain	11	37	1	1	-	-	-	-	-	-
pas-man	-	7	25	-	7	-	1	-	6	4
pot	2	2	25	2	4	3	2	10	-	-
ban	1	19	8	-	4	12	1	4	1	-
chow	1	2	4	-	4	39	-	-	-	-
carr	-	12	10	3	10	11	1	1	1	1
lett	2	29	-	4	11	-	-	2	-	2
TOTAL	17	108	73	10	40	65	5	17	8	7

Table 8 (cont'd.)

Species	RO	QO	CP	F	N-O	COB	N-O	QO	CP	F
Erythrocebus										
grain	35	15	-	-	-	-	-	-	-	-
pas-man		out of season: no counts								
pot	-	18	1	-	6	8	-	8	9	-
ban	-	4	4	-	4	3	3	13	18	1
chow	-	4	11	-	2	9	2	5	17	-
carr	1	10	12	1	8	6	7	2	3	-
lett	-	19	-	19	11	-	-	-	-	1
TOTAL	36	70	28	20	31	26	12	28	47	2

*Abbreviations of foods are as follows:

pas-man = passion fruit, mango
pot = potato
ban = banana
carr = carrot
lett = lettuce

Table 9

Totals and Percentages of Frequency Counts

Species	RO	QO	CP	F	N-O	COB	N-O	QO	CP	F
Ascanius	2	115	75	7	88	30	11	-	9	13
Mitis	14	115	84	29	44	29	8	4	23	-
Neglectus	22	110	85	8	64	27	11	3	20	-
Aethiops	17	108	73	10	40	65	5	17	8	7
Erythrocebus	36	70	28	20	31	26	12	28	47	2
TOTAL	91	518	345	74	267	177	47	52	107	22
	GRAND TOTAL FOR ALL SPECIES:						1700			
Percent of Total Observations by Species										
Ascanius	.1	6.7	4.4	.4	5.1	1.7	.6	-	.5	.7
Mitis	.8	6.7	4.9	1.7	2.5	1.7	.4	.2	1.3	-
Neglectus	1.2	6.4	5.0	.4	3.7	1.5	.6	.1	1.1	-
Aethiops	1.0	6.3	4.2	.5	2.3	3.8	.2	1.0	.4	.4
Erythrocebus	2.1	4.1	1.6	1.1	1.8	1.5	.7	1.6	2.8	.1
Percent of Total Observations - All Species										
Single Positions	5.3	30.4	20.2	4.3	15.7					
Double Positions						10.4	2.7	3.0	6.2	1.2

flexion of the pollical digit and the phalanges lose stability - a distinct disadvantage. The frequency of CUP is lower than that of QO for all species, because although more easily maintained than the RO, it is still less secure than the QO which presses the object against a stable surface.

The E.patas have the lowest percentage of single hand CUP use of all the species studied, not only because there were no counts on passion-fruit and mango, which elicit this grip, but because like the C.aethiops (in their use of the COB), E.patas prefer to use two hands for foods cut into slices or of linear dimensions, perhaps because the hands of a terrestrial animal are held horizontal and equidistant from each other in locomotion and sitting while those of arboreal species are aligned one above the other as in climbing or holding a branch with one hand while sitting.

The N-O and FIST were used almost exclusively for long foods, such as the carrot, where a powerful grip is most functional. Its low frequency of use with banana and sweet potato, both initially long foods, was due to the fact that these were chewed into bits which were better handled by the Quasi-Opposed or CUP as mentioned above.

It is rather surprising that the N-O, a grip in which the thumb is functionless, was favored over the FIST, where the distal pad of the thumb pressed against the dorsal aspect of the distal phalanges. This finding serves to maintain

Table 10

An Inventory of the Individual Living Monkeys
Studied at the United States Primate Center

	Holloman		Tulane Delta	
	Male	Female	Male	Female
M.mulatta	3010	3009	849	691
	3037	563		687
	M88	559		93
	54D	3039		
	277			
	80C			
P.doguera			408	510
			421	68
			419	

Table 11

Counts of Grip Frequency per Food Category
Macaca Mulatta, Papio Doguera

	RO	QO	CP	F	N-O	QO	N-O	F	CP
					M.Mulatta				
Holloman									
Apple bits	10	18	16	1	-	-	-	-	5
Pellet bits	26	12	11	-	1				
Banana bits	1	22	12	3	3	1	-	8	
Tulane									
Grain	33	10	7						
Totals	70	62	46	4	4	1	-	8	5
				GRAND TOTAL 200					
				P.doguera					
Grain	159	34	7						

Table 12

Totals and Percentages of Frequency Counts

	RO	QO	CUP	F	N-O	QO	N-O	F	CP
				Totals					
M.mulatta	70	62	46	4	4	1	-	8	5
P.doguera	159	34	7	-	-	-	-	-	-
				Percentages					
Single Positions									
M.mulatta	35	31	23	2	2				
P.doguera	79.5	17	3.5						
Double Positions									
M.mulatta						.5	-	4.0	2.5

the object more securely in the hand. However, the percentages of QO and CUP were larger than the N-O, suggesting that control was favored over strength.

C.ascanius and *C.neglectus* show the highest frequencies of non-thumb use. In the case of the former, it is because the thumb seems less efficient an instrument as evidenced by lowest frequency of RO. In the case of *C.neglectus*, however, it seems that the digits, having strong grips in themselves, do not require the additional advantage of the thumb.

The total number of double grips, 405, equal only 23.85% of the total observations. This is because the animal chose to assume complementary rather than identical grasps when using both hands. These complementary usages were highly individual both as to animal and food, and were combinations of all the single grips excepting the RO. Thus, CUP and Quasi-Opposed; CUP and Non-Opposed; FIST and Quasi-Opposed, etc. In each case, however, one hand served as support, while the other functioned as control. For example, a monkey may have picked up a carrot with his right hand, probably in the QO or N-O position. He would have lead the food to his mouth with the controlling hand, supporting the carrot either in the FIST or CUP position with the other hand. Occasionally, a foot may have also been used either with or instead of the supporting hand.

When identical grips were used, it was the double

CUP (6.2%) or the quite similar COB (10.4%) that was favored. The basic difference between these two grips is the amount of curvature of the phalanges; greater flexion defining the COB grip. Both grips are opposed, as the thumb is flexed and axially rotated to oppose the other digits, securing the object between its distal palmar pad and those of the other four digits. The frequency of use of these grips may perhaps be accounted for by the fact that the antecedent of these grips, both phylogenetically (Napier, 1960, 1961), and ontogenetically (Hines, 1942) (in man, Castner, 1932) is the simple prehensile or grasping position in which the digits converge towards the palm. These grips were most often used in manipulating large, or heavy foods, such as pineapple and chow-chow, fed in lengthwise slices. Both grips were used in eating maize, to steady the ear while the animal brought his mouth down to the food.

The manner in which food was eaten depended not only on the size, shape and covering of the food, but on the size of the animal as well. Thus C.neglectus males, generally the largest males in the sample, would lift maize to their mouths, although even they seldom husked it with their hands. E.patas and C.aethiops whose hands seemed to be the weakest of all those studied, used double grips for eating carrots, potatoes and even bananas, whereas the others used a single grip. While C.neglectus, C.mitis and C.ascanius peeled bananas with their hands, C.aethiops and E.patas preferred to use their teeth, holding the banana with both hands.

C.aethiops and E.patas are both savanna dwellers and can afford to use double grips when eating. Single grips would seem useful to committed forest dwellers, as one hand is left free to steady the animal on the branch.

Observations at Primate Centers in the United States

Food experiments were conducted on Papio doguera and Macaca mulatta at several primate centers in the United States. At Holloman Air Force Base, apples, bananas and monkey chow pellets were broken into bits approximately 1 cm. to 2 cms. long. It was felt that small size and different textures of foods would discriminate the ease and therefore the frequency of true precision, expressed in the Refined Opposition grip. At Delta Regional Primate Center, grain was used for this purpose. The animals accustomed to fabricated food in inch long pellets were first habituated to the novelty and taste of the grain by being given as much as they wanted. The 10" x 12" aluminum tray was affixed to the front of the cage and access to the food gained through the opening left after removal of the standard feeding container (Plate I). Four ounces of grain was placed on the tray and counts of hand position then taken, as described for Cercopithecus species. As Papio doguera were only tested at Tulane, and only on grain, 200 counts rather than 50 were used.

Both Papio doguera and Macaca mulatta scored very high on the RO, the P.doguera utilizing this grip nearly 80% of its 200 trials while the M.mulatta totalled 35% RO for 200 trials.

Anatomical Data:
Osteology of Opposition

The Joints

Opposition is a complex movement involving all three pollical joints: the carpometacarpal, metacarpophalangeal and interphalangeal.

A diarthritic saddle joint (carpometacarpal) is characteristic of all catarrhines (Napier, 1955) except Hylobates whose carpometacarpal joint is a ball and socket (Napier, 1961, p. 127, in a footnote). The articulation of the metacarpal with its carpal the trapezium, in the carpometacarpal joint, permits flexion, extension, abduction and adduction (Haines, 1944). Medial rotation, or conjunct rotation (MacConaill, 1946), a movement essential to opposition, is actually a derivative of these, as rotation first requires flexion of the metacarpal and then abduction of it (Napier, 1966). It is the rotation of the metacarpal which, according to Napier (1961), defines true opposition in the Catarrhini as differentiated from pseudo-opposition in Ceboidea.

The metacarpophalangeal joint, a condyloid or hinge joint, permits full movement: abduction, adduction, flexion, extension and axial rotation. In primates it is this joint which is partially responsible for convergence, the approximation of the fingertips, and divergence, a fanning out of the fingers (Napier, 1961). Because abduction and medial rotation are permitted at this joint, it is responsible for opposition as well (Napier, 1966). Indeed, the total movement of opposition is largely dependent on the medial rotation of this joint which largely determines the positioning of the distal phalanx and its palmar pad.

The interphalangeal joint permits only flexion and extension. Stability is critical to opposition which requires a steady pressure on an object. It is difficult to attain stability at this joint because while some action on this joint is derived by the insertion of intrinsic muscles into the dorsal expansion (Landsmeer, 1949; McFarlane, 1962; Stack, 1962), there are principally only two muscles working over the joint. The distal phalanx can be passively positioned by action of the metacarpophalangeal joint, moving the proximal phalanx. Free movement can occur if pressure is exerted on the distal phalanx or its tip by the second digit. Much exertion is required to stabilize the distal joint.

Carpus

The carpus in primates describes an arch (Fig. 2), the function of which according to Hughes (1944), is "...to stabilize the carpal tunnel in which the flexor tendons lie and thus to facilitate their movement" (p. 172). Napier and Davis (1959) and Napier (1961, 1966, 1967), following Hughes, state that the deepest carpal tunnels belong to those primates who depend more on the use of their flexors, that is, the true, modified and semi-brachiators (Oxnard, 1963). Brachiation is locomotion including "...the use of the forelimb in suspending and propelling the body from above" (Oxnard, 1963, p. 166). While the flexors involved in brachiation are the digital flexors, the curvature of the carpal canal affects the carpal of the pollex.

> The greater the curvature of the carpus as a whole, the more nearly does the set of the trapezium approach a right angle with the plane formed by the posterior margin of the capitate (Napier and Davis, 1959).

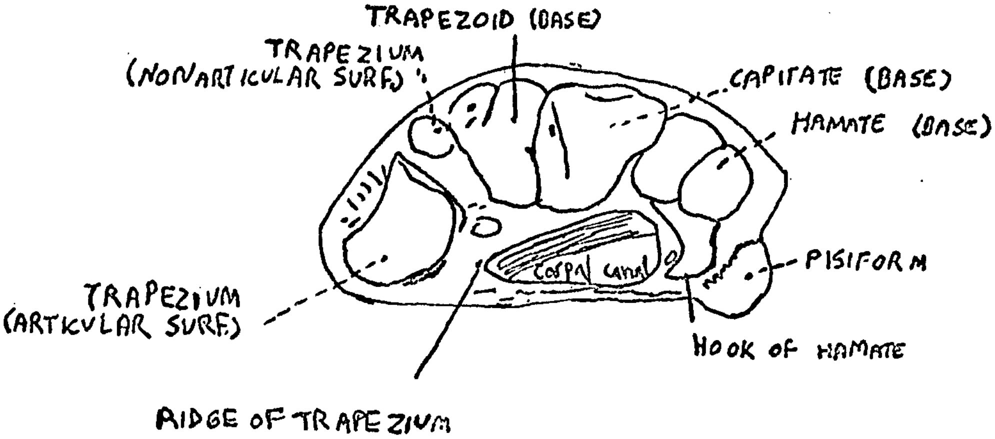
The closer the trapezium lies to a right angle, the more the distal palmar surface of the thumb lies in a position of "Passive Opposition" (Napier and Davis, 1959) to the second digit.

Napier (1961) suggests that the movements forming the substrate of opposition, i.e., convergence and divergence,

Figure 2.

The Articulation of the Carpals and the Carpal Canal

in Homo sapiens



modified from Kaplan, 1953.p.122

relate to some extent to the shape of the metacarpophalangeal joint, but depend on the transverse carpal arch. The deeper the arch, the more the inclination of the trapezium, and consequently the greater the Passive Opposition and therefore the movement of opposition. The deepest arches belong to the species incapable of opposition due to a functionless thumb. This includes the Colobinae, who lack a thumb, and Pan, Gorilla and Pongo who either totally lack a long pollical flexor, or have one very much reduced. Conversely, a shallow arch is found in the guenons and macaques (Napier, 1961) whose opposition is greater than the species mentioned above. Napier attempts to resolve this contradiction by stating that the length of the thumb is of paramount importance. The shorter the thumb, the less able is it to contact the second digit. This relationship is expressed in the "Opposability Index" (Napier, 1961). This explanation is the prevalent one accounting for the lack of opposition in the brachiators (except Hylobates) with a deep tunnel and for the presence of opposition in guenons and macaques (Campbell, 1966; Buettner-Janusch, 1966).

Passive Opposition

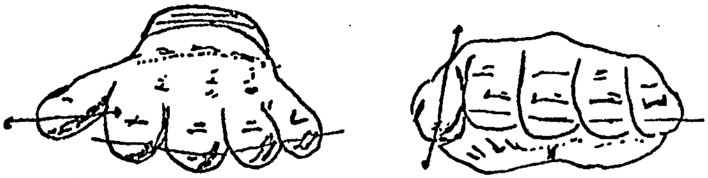
The term "Passive Opposition" (Napier and Davis, 1959) describes the set of the thumb, so that it hangs, when the hand is at rest, with the palmar surface horizontal and parallel to a plane through the heads of the digital metacarpals. The more the thumb metacarpal lies so that its ulnar or inner surface is facing dorsally the more the thumb lies in opposition, and the less muscular activity is needed to complete the contact between the tip of the thumb and the tip of the second digit. The amount of tilting is an important factor in the complex of variables limiting or enhancing opposition. Should Passive Opposition be minimal, the musculature of the thumb would be required to compensate in order to move the thumb into opposition (Table 15).

Passive Opposition can be evaluated as Schultz (1926) has done (Fig. 3), by orienting the hand with the fingertips facing the line of vision, while the hand is resting on the elbow. Kaplan (1953), has evaluated Passive Opposition by looking at the thumbnail, with the hand in the same position. In full Passive Opposition the entire surface of the nail is directed laterally.

The degree of Passive Opposition can also be ascertained by viewing the head of the pollical metacarpal from the dorsum of the hand after dissection, while the arm is resting on the elbow. The more the head of the metacarpal is visible, the less the metacarpal is rotated at its carpal articulation. The styloid process of the metacarpal is directed through the midline of the trapezium, rather

Figure 3.

The Rotation of the Thumb Viewed From the Fingertips



8 WEEK FETUS

ADULT

H.sapiens

from Schultz, 1926. p.495

than medial to the tubercle towards the ulnar side of the carpal. The extent of Passive Opposition is a function of the articulation of the metacarpal with its carpal the trapezium, and of the trapezium with the trapezoid os centrale and scaphoid.

Napier maintains that it is the angulation of the trapezium to the other carpals which determines the amount of Passive Opposition of the thumb. He has measured this relationship by drawing a line through the articular surface of the trapezium intersecting a line through the dorsum of the capitate. The resulting angle approaches 90 degrees in Papio, while for Cercopithecus it measures 60 degrees (Napier and Davis, 1959); no measurements were taken of Macaca. The difference between these measurements of genera supports the observations made of the use of the hand discussed earlier, i.e., that higher frequencies of R-O were found in Papio than in Cercopithecus species.

Differences between species of Cercopithecus, however, are not revealed in this measurement. Observations of the metacarpal reflect differences in the use of the hand between species. Viewed from the fingertips, the distal surface of the thumb appears rotated in all species studied. But viewed from the dorsum of the hand, in dissected and fleshed specimens, the torque visible is seen to be a function of the articulation of the proximal phalanx with the head of the metacarpal, and not due to the nature of the metacarpal articulation with the trapezium. This is confirmed in analyzing dissected but still articulated specimens. In C.mitis and C.neglectus both the head and base of the metacarpal could be seen when the hand was viewed from the dorsum. In these two species, the lateral side of the trapezium articulates with the radial aspect of the trapezoid so that these two carpals are level. However, in C.neglectus, the inner or ulnar side of the trapezium is tilted slightly dorsally, but is checked by the radial ridge of the trapezoid. In C.aethiops only the head of the metacarpal is visible, with the ulnar aspect most obvious, and the metacarpal is slightly twisted. The articular surfaces of the trapezium are not completely level with those of the trapezoid since the trapezium is slightly tilted dorsally. This is not the case in E.patas. Viewed from the fingertips, the thumb appears to lie on its side, and this is confirmed in the dissected hand, where it can be seen that the metacarpal is rotated on the trapezium so that the ulnar border of the bone is seen when the hand is viewed from its dorsum. The trapezium is inclined with its ulnar aspect tilted dorsally.

It is this latter configuration which is present in the Papio and Macaca specimens studied. X-rays of Macaca mulatta pointed out the degree to which the styloid process of the metacarpal was directed ulnarward of the tubercle of the trapezium. A greater degree of Passive Opposition exists in these two genera due to the articulation of the metacarpal with the trapezium in such a fashion that the styloid process is directed ulnarward, not palmarward. As the pollex lies already passively opposed to the second digit in the Position of Rest, less action is required to move the pollex into contact with the tip of the second digit. This structural fact is reflected in the high frequencies of Refined Opposition counted for these two genera.

Opposability Index

It has been stated that the guenon or Cercopithecine thumb is destined to atrophy, rather like that of the Colobinae (Schultz, 1926; Ashley-Montagu, 1931; Oxnard, 1963). Schultz (1926) noted that the "future fate of the guenon hand..." (p. 494) is foreshadowed by its present state. That is, there will be an evolution of thumbs so short that they "...can be of little use" (p. 494). The factor causative of this reduction is, according to Ashley-Montagu, arboreal existence. The exigencies of this adaptation foster specializations including the loss of the thumb.

The distinction Napier makes between habitat and mode of locomotion is developed by Oxnard (1963). He notes that monkeys which progress quadrupedally in trees or on the ground have thumbs substantially longer than those of semi- or true brachiators.

Schultz (1926) noted that the embryonic thumb "... branches at a place favorable for effective opposability" that is, from the palm immediately at the base of the second digit, and that it is "...not yet rotated around its longitudinal axis to face the other digits" (p. 495). The thumb, however, migrates proximally "...to a place nearer the wrist" (p. 495) in the course of growth. Jouffroy and Lessertisseur feel that this ontogenetic development is phylogenetic as well, as in those animals where true opposition does not exist, the thumb inserts very close to the base of the second digit (1960).

A study of the collection of rhesus fetuses stained with Alizarin, in the collection of Dr. Daris Swindler, confirms Schultz's observations that the thumb appears to shorten, but although there is no longitudinal rotation of the metacarpal, the phalanges appear to be rotated ulnarward. The thumb of specimens with Crown Rump lengths 95 mm, 110 mm, and 130 mm show the metacarpal appearing to branch from the level of the base of the second digit. As only a segment of the proximal third of the metacarpal has ossified and therefore stained, it was impossible to ascertain the true relationship of the pollical metacarpal to the trapezium, or to the second metacarpal. What did seem clear, however, was that the distal phalanx is rotated before the proximal, and the latter before the metacarpal, simulating very closely what Napier (1961) has formulated as the phylogenetic route from prehensility through pseudo-opposability (metacarpophalangeal joint) to true opposability (carpometacarpal joint), and which is reflected in the ontogeny of manipulative behavior in H.sapiens (Castner, 1932).

Napier (1961, 1966, 1967) believes that the primary modification of opposability in Cercopithecoidea is evidenced in the Opposability Index. Perfect opposition, "...ultimately rests upon the proportionate lengths of the thumb and index fingers" (1961, p. 120).

Measurements taken in the present study suggest a modification of this view. Low ratios appear with high ratios in the same species (Table 14). For example, in C.mitis the range runs from 48% to 55%, the lower figure taken from an adult male, yet the performance of C.mitis did not vary substantially from individual to individual. A high average of ratio per species did not correlate with high Refined Opposition frequency (Table 16). Napier's figures on E.patas (N=3) average 42% Opposability Index, while the sample of this study (N=4) average 55.4%. The difference between the two samples may be related to the fact that the sample of animals in this study which were received from Kabate veterinary hospital, were female and most juvenile, the index decreasing with maturation (Schultz, 1926). Nevertheless, the range fell well within that of Napier's. *E.patas* had a Refined Opposition grip frequency of 2.1% of the total observations, the highest for all species studied in Africa. Yet their thumbs measure among the shortest, when Napier's figures are joined to those of the present study.

C.mitis, *C.aethiops* and *C.neglectus* have averages quite similar to each other, 51.1%, 51.9% and 51.8% respectively, yet their performances vary radically. *C.mitis* has a Refined Opposition grip frequency of only .8% while *C.aethiops* and *C.neglectus* registered 1.0% and 1.2% Refined Opposition grip, respectively (Table 13).

The Opposability Index has been accepted as the limiting factor in opposability (Jolly, 1964; Hall, 1966; Campbell, 1966; Buettner-Janusch, 1966). When, however, performance is evaluated in terms of this Index, it must be concluded that the lengths of the digits are pertinent but not decisive in determining the degree of opposition which a species of monkey exhibits.

Table 13

Opposability Index

Species	N	Average	Range
H.sapiens	7	69.6	63 - 75.9
C.mitis	7	51.1	48 - 55
C.aethiops	8	51.9	50.8 - 53
C.neglectus	6	51.3	50 - 53
E.patas	4	55.4	52.4 - 58
<u>From Napier (1967)</u>			
Cercopithecus	11	53	48 - 55
Papio	13	57	53 - 60
Macaca	18	54	48 - 59
E.patas	3	42	57 - 57

Table 14

The Complete Sample for the Opposability Index

Species		Species Average	Species		Species Average
C.mitis			*E.patas*		
Sykes					
male adult M.P.	48		KAB. e.p. 1	58	
AB 4	55		fem.juv.		
LIM 2	51		KAB e.p.2	54.9	
		51.1	fem.juv.		
Blues					55.4
KT 93	49		KAB. e.p.3	56	
KT 91	55		fem. ad.		
KT 84	53		KAB. e.p. 4	58.1	
C.aethiops			*H.sapiens*		
Male ad. M.P.	53		fem.18 yrs.	65	
MAG 1.	53.1		fem.27 yrs.	67.9	
Male ad. M.P.	51.7		fem.23 yrs.	63	
Fem. ad. M.P.1	50.8	51.7	male 24 yrs.	75.9	69.6
Fem. ad. M.P.2	50		male 56 yrs.	70	
Male ad. KAB.	52.4		male 22 yrs.	73	
			male 19 yrs.	72.4	
C.neglectus					
MHS 19	51				
KAB. n.1.	50				
Fem.ad.					
KAB n.2.	53				
Male ad.					
KAB n.3.	52	51.3			
Male ad.					
KAB n.4.	50				
Male sub.					
KAB n.5.	51				
Fem. ad.					

LEGEND:
MAG, AB, LIM. - spec. symbols for Tigoni collection
M.P. - spec. symbols received via Museum for Prehistory
KAB. - spec. symbol received from Kabate veterinary hospital.

NOTE:-- All readings on left hand. H.sapiens readings on live individuals.

No *C.ascanius* available

Anatomical Data
Myology of Opposition

Introduction

Dissections were made to attempt to ascertain why the use of the hand of the species of Cercopithecoid monkeys studied varied so markedly. The myological variations found tend to correlate with the observations of grip frequency made earlier. These variations include: (1) all species differing from one another, and (2) some species clustering, but collectively differing from the remaining species.

Carpo-Metacarpal Joint

The complex of movements permitted at this joint are brought about by four muscles: the abductores longus et brevis, the opponens pollicis and the flexor pollicis brevis (Plate III).

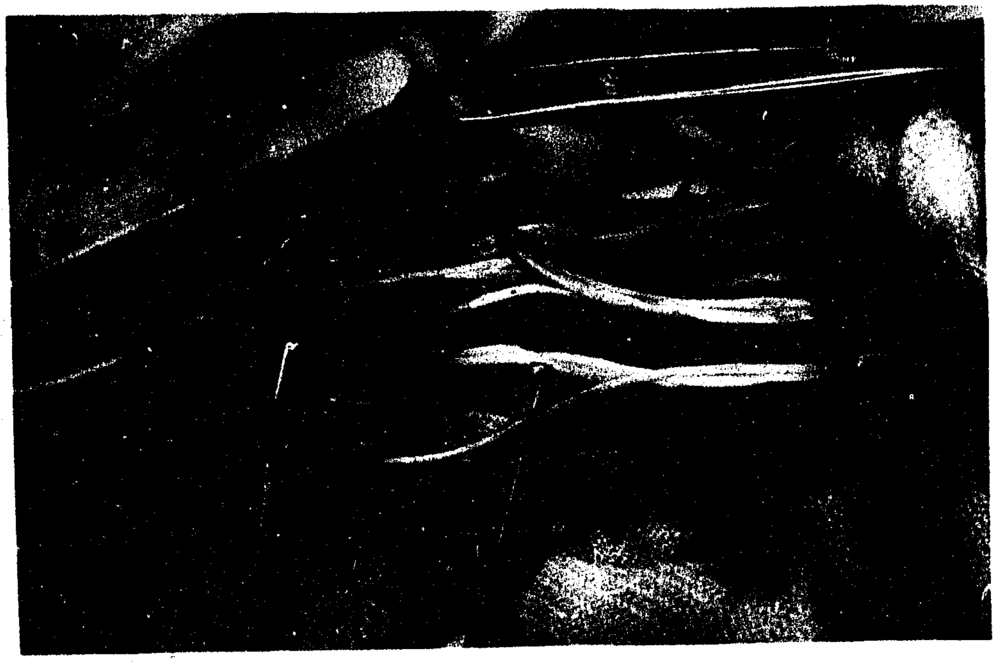
The opponens pollicis, in all species of Cercopithecoidea studied, originated from the flexor retinaculum and the ridge of the trapezium and scaphoid and inserted on the medial to radial aspect of the head of the metacarpal.

A slight variation was found in *C.neglectus*, where the opponens received a tendon from the abductor longus-extensor brevis complex. The addition of these fibers may be partial explanation for the ease with which *C.neglectus* assumed the Refined Opposition grip, as their exertion conjointly with the opponens would enhance stability of the metacarpal, and increase abduction so the opposition would be facilitated. The insertion for C.neglectus is quite similar to that described for the other Cercopithecus species, except that the opponens belly is more pronounced, bunched proximally, and sends a long thin tendon to insertion increasing leverage. The muscle is very slim in C.mitis and C.aethiops (Plate III), appearing almost translucent.

The muscle has the same origin and insertion in E.patas (Plate III) as in Cercopithecus. The specimens of Papio doguera and M.mulatta showed a similar pattern: the opponens running deep to the abductor brevis and flexor pollicis brevis, as it does in all Cercopithecoid species, originated from the flexor retinaculum and trapezium, with some fibers occasionally from the scaphoid, and inserted on the head of the metacarpal, towards the lateral aspect (Plate III). In Papio, the muscle attached along the length of the metacarpal, perhaps thus gaining more mechanical advantage.

Day and Napier (1963) have discussed the phylogenetic significance of the deep head of the flexor brevis and have found it to exist in Cercopithecoidea, being especially well developed in M.mulatta. They noted the probable phylogenetic migration of the deep head from an attachment on the ulnar

Plate III. Flexor Brevis (5), Opponens Pollicis (4), Abductor Brevis (3)

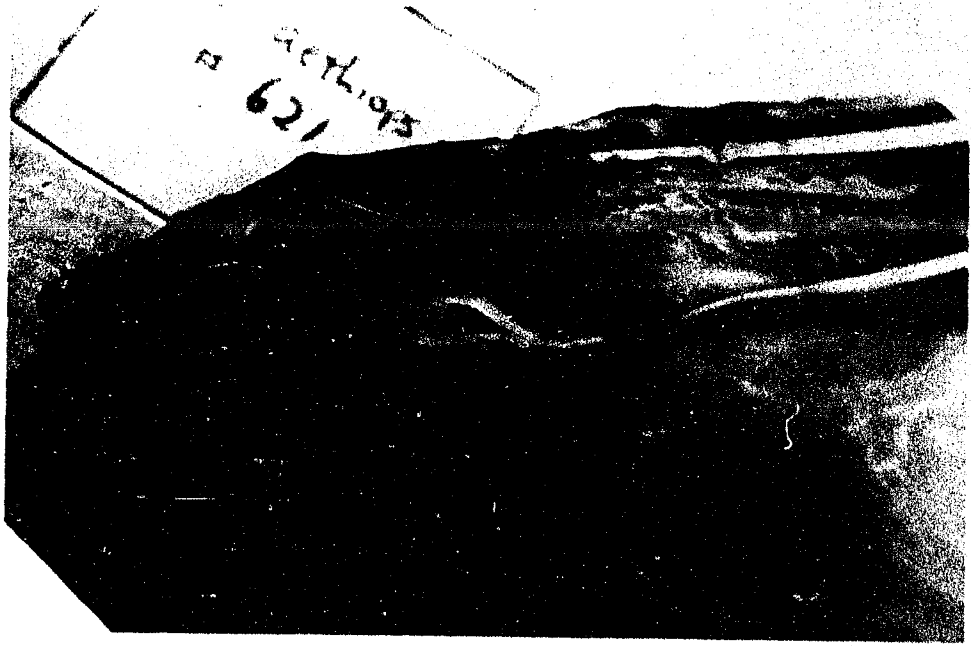


E.patas

P.doguera

Plate III. Flexor Brevis, Opponens Pollicis, Abductor Brevis (5, 4, 3)

M.mulatta



C.aethiops

sesamoid to an attachment on the radial sesamoid and remarked that this migration seemed related to the "acquisition of true opposability in catarrhines" (1963, p. 122). In the specimens of Cercopithecoidea studied, there seemed to be great variation in this muscle, even between the two arms of one animal (M.mulatta, #579), which coincides with the evolutionary history of this muscle (Day and Napier, 1961, 1963).

The two heads of flexor brevis were most clearly defined in the specimens of Papio, and least clear in Cercopithecus. Where there were two heads present, the superficial head originated from the retinaculum and trapezium, and the deep head (the more medial one), from the flexor retinaculum and trapezoid (P.doguera, M.mulatta, E.patas, C.neglectus). Both heads inserted on the proximal phalanx, the medial head attaching to the head of the metacarpal as well. The fibers of the two heads were often found to be intertwined (P.doguera, M.mulatta and E.patas) and sometimes only one head was discernible (C.mitis, C.aethiops, C. neglectus, E.patas, M.mulatta).

The abductor brevis, whose principal actions are on the proximal phalanx of the thumb (Wood-Jones, 1920), has generally been considered to be most responsible for opposition (Duchenne, 1856; Wood-Jones, 1920; Napier, 1952; McFarlane, 1962). The abductor brevis showed little variation in all the species of Cercopithecoidea studied. It originated from the flexor retinaculum, the tubercle of the scaphoid and the crest of the trapezium, and inserted on the lateral base of the proximal phalanx with fibers moving into the dorsal expansion. Differences between origin on both scaphoid and trapezium occurred, but as these were equally within species as between species, do not seem significant.

The abductor pollicis longus is known in the earlier literature as the extensor ossis metacarpal pollicis (Primrose, 1899; Wood-Jones, 1920: Straus, 1941) and has been identified as homologous with the supinator manus of reptiles and amphibians (Straus, 1941).

The abductor pollicis longus cannot be discussed in non-human primates without reference to the extensor pollicis brevis. Most authorities maintain that there is no extensor brevis in catarrhini (Polak, 1908; Jouffroy and Lessertisseur, 1960) although Straus (1941), who subscribed to this view, also noted that it is occasionally found in gibbons and gorillas.

Wood-Jones stated that rather than seeing the extensor pollicis brevis as new in higher catarrhini, including man, it is more true to say that separation of the extensor pollicis brevis from the abductor longus is fully realized in man. This latter view was substantiated in dissection of 41 specimens of Cercopithecidae where it was found that

Table 15

Articulation of the Metacarpal: Passive Opposition

	Head of Metacarpal	Base of Metacarpal	Relation of Trapezium to Trapezoid	Trapezium
C.mitis	facing dorsally	facing dorsally	level	level
C.neglectus	facing dorsally	facing dorsally	not completely level	ulnar side tilted dorsally
C.aethiops	facing dorsally but ulnar aspect most obvious	tilted ulnarward	not completely level	same as above
E.patas	same as above	same as above	not level	meta fully rotated on trapezium
M.mulatta	tilted ulnarward	same as above	same as above	same as above
P.doguera	same as above	same as above	same as above	same as above

Table 16

The Overlap of Opposability Index and Performance

```
Refined Opposition
   Performance

                                              -----H.sapiens---------

Very High                  Papio (Napier)

               _Macaca (Napier)_____


             _E.patas (Napier_____
High
                        E.patas (Burton)

                 C.neglectus

Medium           C.aethiops_



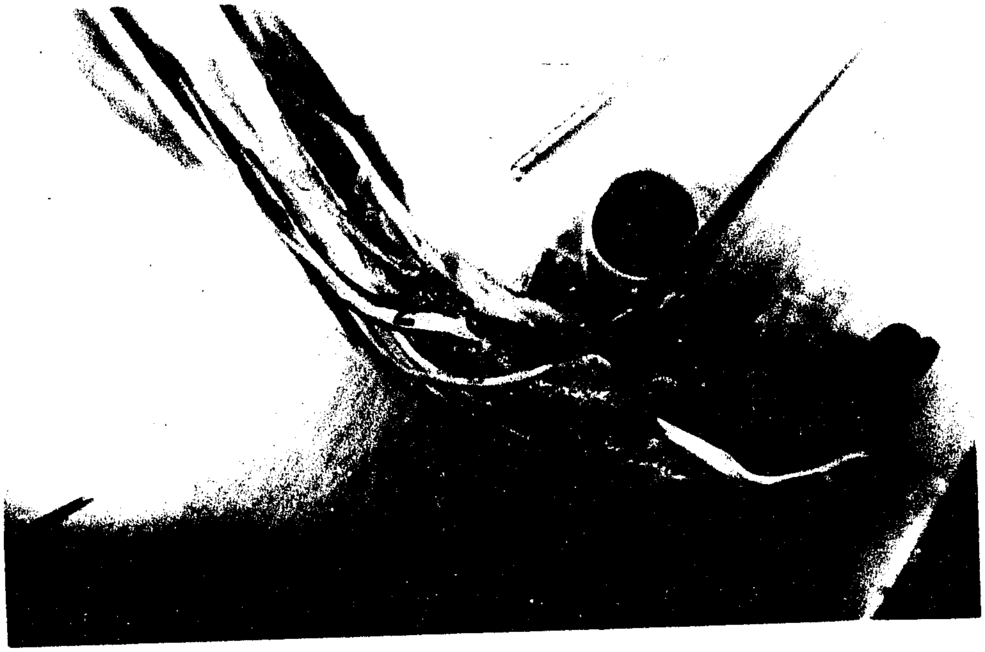
               __C.mitis______
Low
           46  48  50  52  54  56  58  60  62  64  66  68  70  72  74
                        Opposability Index in Per Cent
```

there is a tendency in some of the species towards separation of the extensor. In the present study, the degree of separation was found to coincide with higher frequency of Refined Opposition grip.

The abductor longus and the extensor brevis form a muscular complex (Plate IV). They either originate as one muscle, or as two very much joined. They insert as a unit even when the fibers of the two can be distinguised. In general, the abductor-extensor complex originates high on the posterior surface of the forearm, between the radius and ulna, with the abductor portion more proximal. The complex then passes down the forearm, usually attaching onto the dorsum of the trapezium, the outside or radial side of the base of the thumb metacarpal, and on into the flexor retinaculum on the ventral side of the hand. When the fibers can be separated, slips or fibers of both abductor and extensor insert onto the base of the metacarpal, trapezium, sesamoid and retinaculum. All the species do not have all the attachments as discussed below. A designation at the carpal-metacarpal region of fibers as abductor or extensor is made. The fibers and tendon deriving from the radial portion of the mass on the forearm were termed "extensor," while those from the ulnar portion of the mass were termed "abductor."

Polak ssserted that there was no extensor brevis in

Plate IV. Abductor-Extensor Complex (2)

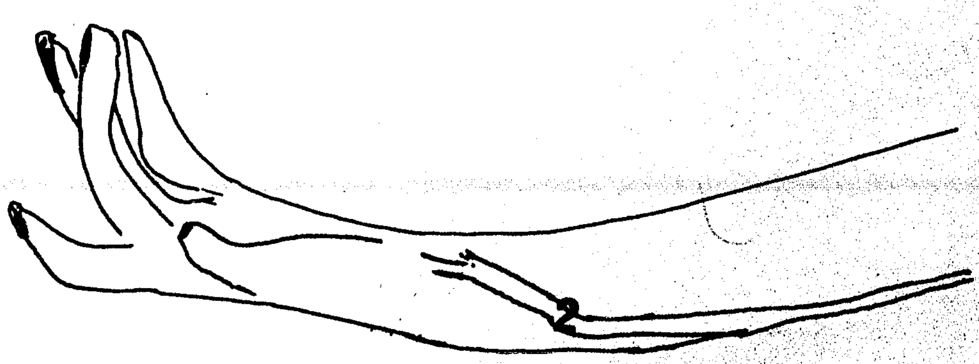


C.aethiops

the Colobus specimens she examined. Yet in four specimens dissected at Tigoni, although the extensor was so fused with the abductor that the fibers could not be separated, the extensor portion of the joint tendon could be demarcated. This was also the case with C.mitis; the two tendons insert as an intertwined unit onto the sesamoid and base of the metacarpal and the trapezium, but the extensor portion remains a visible entity.

In C.aethiops (Plate IV), the abductor and extensor are separate at origin. The abductor crosses over the extensor and joins it to form a tendon which inserts on the sesamoid and retinaculum and the base of the metacarpal as the base of a triangle (Plate IV). The extensor portion is again separable from the abductor and inserts onto the trapezium, across to the base of the metacarpal, and onto the sesamoid and retinaculum. In C.neglectus as in C. aethiops, the tendons coming from the joint mass insert as one but can be separated. The abductor overlies the extensor and can be seen as a distinct tendinous portion slightly above the carpals. It inserts on the lateral, almost ventral side of the base of the metacarpal. Some fibers attach onto the sesamoid and retinaculum, and some fibers onto the opponens pollicis. The extensor inserts by a minor slip onto the trapezium, and then passes a major slip over to the base of the metacarpal, sesamoid and retinaculum, insert-

Plate IV. Abductor-Extensor Complex (2)



E.patas

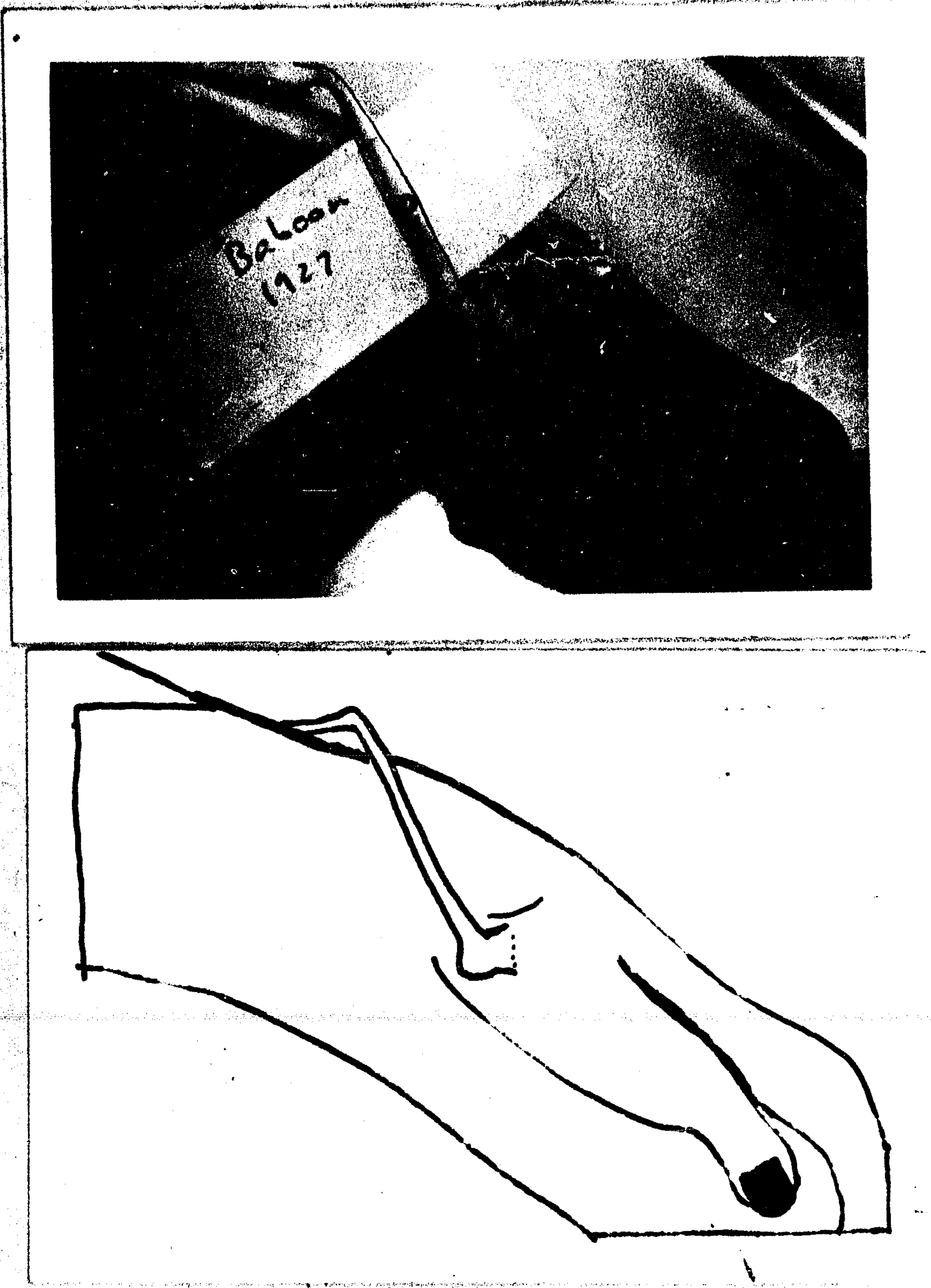
ing underneath the abductor.

E.patas is somewhat different in insertion (Plate IV), in that a major slip from the abductor inserts onto the sesamoid and retinaculum, and a major slip from the extensor inserts onto the base of the metacarpal, but a secondary, minor slip emerges from the major tendons to insert the extensor on the sesamoid and retinaculum, and the abductor on the metacarpal distal to the insertion of the extensor; there seems to be no attachment onto the trapezium. As with C.aethiops, there is a separate origin for each muscle.

While the high Refined Opposition performance in P.doguera seemed to suggest a further development of separate muscles, this expectation was not confirmed at dissection. The muscle mass originated high on the ulna, and immediately crossing to the radius, descended the forearm. The tendon inserted as one unit as the base of a triangle, whose left leg, the abductor portion, attached to the sesamoid and the trapezium. The tendon could be separated at the level of the carpal end of the radius, but neither the muscle fibers nor the inserting tendon could be separated (Plate IV).

The M.mulatta specimens were like Papio doguera in origin (Plate IV), but rather more like C.aethiops and C.neglectus in insertion (Plate IV). At the base of the muscle belly, approximately 2 millimeters from the carpals, two tendons were separable. The abductor portion inserted

Plate IV. Abductor-Extensor Complex (2)



P.doguera

on the sesamoid and trapezium, and the extensor portion on the base of the metacarpal, but the two tendons did insert as one triangular piece.

In terms of opposition, the differences in origin and insertion of the abductor-extensor complex are significant. When the extensor brevis is functionally totally lacking (as in Sykes and Colobus), the actions of this muscle are of course, not available. Where the extensor exists as tendinous fibers of insertion (Macaca mulatta, C.neglectus), independent only at insertion, and otherwise closely intertwined with abductor fibers, contraction of the abductor triggers the extensor fibers to act and from their attachment on the radial side of the base of the metacarpal, extend dorsally and slightly abduct the metacarpal. The separate abductor portion of the common insertion on the carpal acts as an abductor of the hand, though in those animals where there is a metacarpal insertion as well (C.neglectus, C.aethiops, E.patas) the abductor portion can aid in stabilizing the metacarpal. The configuration of the complex in C.aethiops and E.patas is similar: separate origin and separate insertion of the two masses. However, as the extensor brevis does not insert on the base of the proximal phalanx, opposition in these animals must also be more difficult to attain since stability of the metacarpophalangeal joint can only be achieved by residual effort of

Plate IV. Abductor-Extensor Complex (2)

M.mulatta

the intrinsic muscles inserting into the dorsal expansion. Furthermore, since the abductor attaches most consistently to the trapezium and sesamoid, rather than to the metacarpal itself, stability at the carpometacarpal joint is curtailed, and abduction from this muscle minimal.

Metacarpophalangeal Joint

Movement at this joint, flexion, extension, abduction, adduction and axial rotation, are fundamental to the movement of opposition, as the proximal phalanx is twisted medially, resulting in functional rotation of the digit. The muscles involved are abductor pollicis brevis, flexor pollicis brevis, extensor pollicis brevis and adductor pollicis. The first three muscles have been discussed in the preceding section, as they either act over the carpometacarpal joint (abductor brevis, flexor brevis), or relate to a muscle that does (extensor brevis).

The adductor pollicis acts on the metacarpophalangeal joint to draw the digit to the hand. In terms of opposition, the function of adductor pollicis is as stabilizer of the thumb (Napier, 1966). Force exerted by the second digit is counteracted at the metacarpophalangeal joint so that the head of the metacarpal and the base of the phalanx are firm.

The adductor is comprised of two heads: the oblique and the transverse. The transverse originates on the palmar surface of the third metacarpal, and the oblique at the base of the second and third metacarpals and on the capitate carpal at the base of the third metacarpal. These heads join into one tendon at insertion on the medial side of the base of the first pollical phalanx. The origin of both the transverse and oblique portions of the adductor is the same in all the Cercopithecinae studied. In *Colobus abysinicus*, the adductor has no apparent function: the muscle is disproportionately large and seemingly serves only to immobilize the thumb and unite it to the hand. The transverse head originates on the lateral aspect of the base of the fourth metacarpal, and the oblique has an extra head that originates on the lateral base of the fifth digit. Both heads insert all along the proximal phalanx.

In all Cercopithecinae studied, the oblique and transverse heads of the adductor insert separately but with minor variations. *C.aethiops* inserts the transverse from the head of the metacarpal to the base of the proximal phalanx, and the oblique on the lateral aspect of the head of the metacarpal. The insertion of both of these is similar in *C. mitis*, but the oblique is a stouter muscle than in *C.aethiops*.

The insertion of these two parts of the adductor in *E.patas* and *C.neglectus* is on the lateral aspect of the head of the pollical metacarpal, and the transverse is a very thin muscle. In *C.neglectus* it is still visible as a muscle, but in *E.patas*, it merely consists of muscle fibers in connective tissue. In *M.mulatta*, the transverse attaches lower on the metacarpal shaft than does the oblique; from the middle of the metacarpal shaft to the base of the 1st phalanx. The oblique attaches to the head of the metacarpal and the base of the 1st phalanx.

Papio doguera differs from the other species described in that the distance between the two heads of the adductor is very great. The transverse head inserts on the metacarpal and onto the medial aspect of the base of the 1st phalanx while the oblique inserts on the head of the metacarpal and into the insertion of the transverse.

There is a strong correspondence between the weakness or slimness of the transverse head of the adductor and high Refined Opposition performance. In *Cercopithecus* species *aethiops* and *neglectus*, whose performance is markedly higher than that of *C.mitis* or *C.ascanius*, the transverse head is, in comparison to the oblique, extremely poorly developed. This is also the case in *E.patas*, where the transverse is so reduced as to appear merely as isolated fibers with a connective tissue matrix. In *Papio doguera*, the two heads are distinct from each other, appearing more as separate muscles than as two heads of the same muscle. The oblique is better developed than the transverse head.

The extreme case of a developed oblique is seen in *Colobus abyssinicus* where that head of the adductor unites the thumb to the hand itself. It seems that development of the transverse head, by securing the pollex to the rest of the hand alongside d2, counteracts the advantage of a high degree of Passive Opposition.

Interphalangeal Joint

There are only two muscles that work over this joint whose role in opposition is very important. These are the flexor pollicis longus and the extensor pollicis longus (Plate V). The extensor longus is a "real muscle in principle" in primates (Jouffroy and Lessertisseur, 1960, p. 128). Its origin is on the posterior aspect of the ulna and adjacent interosseous membrane distal to the abductor longus in all species except Colobus abyssinicus. In this species, the extensor originates as a part of the abductor longus-extensor brevis complex, or from the extensor indicis (Jouffroy and Lessertisseur, 1960), or is entirely lacking (Polak, 1908). The insertion for all species except Colobus abyssinicus is to the base of the distal phalanx. In Colobus abyssinicus, it inserts on the tip of the only phalanx, or onto its shaft (Jouffroy and Lessertisseur, 1960).

The extensor pollicis longus extends the distal phalanx of the thumb, and pulls the entire digit dorsad. It is an antagonist to the opponens pollicis (Wood-Jones, 1920) as it can rotate the thumb dorsally. Its primary function is to exert a counterforce against the flexor pollicis longus. When these two muscles act, they stabilize the interphalangeal joint and maintain the distal phalanx.

In Cercopithecidae, the flexor longus arises as a tendon from the flexor digitorum profundus mass. Its degree

Plate V. Flexor Pollicis Longus (1)

E.patas

M.mulatta

of independence from the mass does vary. In E.patas, this origin is considerably more proximal than it is in the Cercopithecus species, coming from the flexor digitorum profundus at the carpals rather than from the palm (Plate V). This origin is also found in M.mulatta (Plate V), but not in Papio doguera, where the flexor longus originates above, that is, more proximal than the carpals (Plate V).

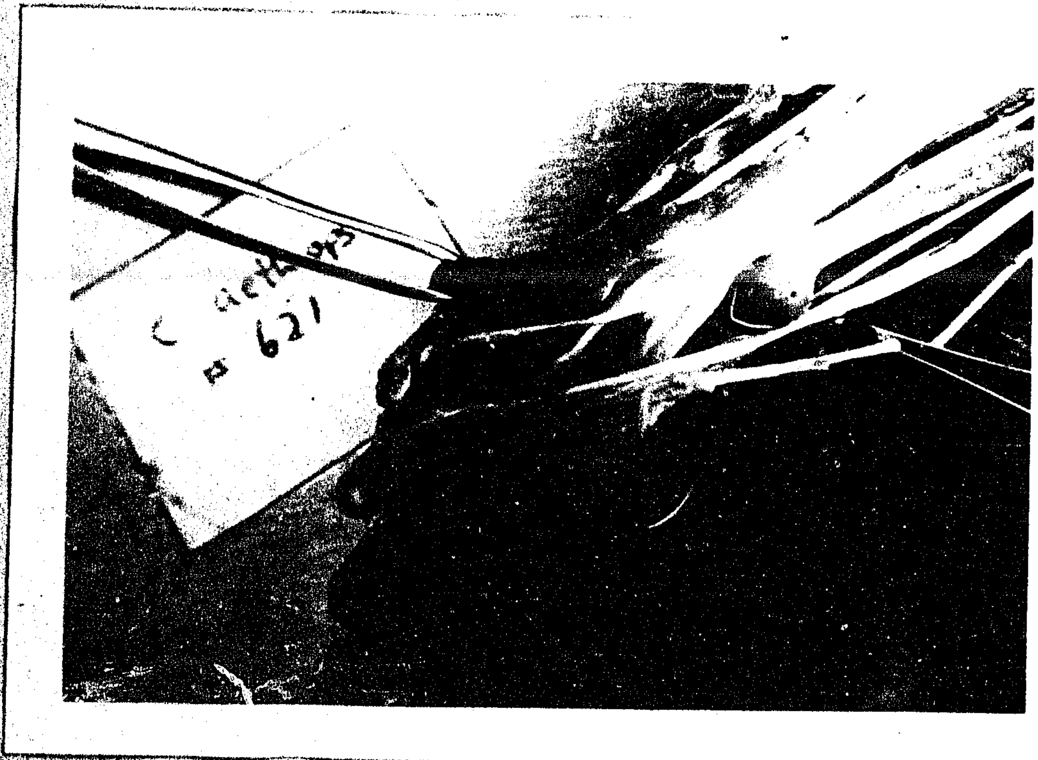
The origin at the palm for Cercopithecus species is generally from the center of the group, or slightly radial, although in two specimens of C.aethiops, it came from the ulnar side (Plate V).

The insertion of this muscle was the same for all specimens of Cercopithecidae studied, i.e., at the very tip of the distal phalanx.

The flexor pollicis longus works in direct opposition to the extensor longus. It flexes the terminal joint of the thumb and has a limited effect on the proximal joint as well. In opposition when the palmar pad of the distal phalanx of the thumb contacts the distal palmar pad of the second digit, the exertion of the flexor longus stabilizes the terminal phalanx at the interphalangeal joint, and thus permits manipulation of an object (Napier, 1966; Kaplan, 1953). When the thumb has moved into a position of opposition, but is not contacting the second digit, it is the mutual exertions of the two long muscles that hold the terminal phalanx

Plate V. Flexor Pollicis Longus (1)

P.doguera



C.aethiops

firm. The insertion of the flexor longus into the tip of the distal phalanx in all the Cercopithecidae studied, results in loss of control of the interphalangeal joint.

The significance of this insertion is that "the half of the pincers formed by the thumb lose the power to hold the distal phalanx of the thumb against the distal phalanx of the index finger" (Kaplan, 1953, p. 10). This reduction in efficiency is due to the fact that contraction along the flexor longus will result in curling over the distal phalanx. As the counterforce exerted by the extensor longus is to the base of the distal phalanx and <u>not</u> the tip, there is no means of inhibiting this action of the flexor. That his curling does occur is observed in the variation of the Q-O described above where the ungular surface of the thumb is pressed against the side of d2 rather than to the volar surface of d2 (Table 17).

Table 17

Summary of Origin and Insertion of Pollical Muscles

Muscle	Origin	Insertion
P.doguera		
Extensor pollicis brevis	rad. to ulna. as one with abd. longus	metacarpal and trapezium as one with abd. longus
Extensor pollicis longus	Post. aspect ulna. and adjacent interos memb. distal to abd. longus	Base of the distal phal.
Opponens pollicis	Flexor ret. and trapezium occasionally some fibers from scaphoid	Head of the metacarpal and along entire length
Flexor pollicis longus	Superficial aspect flex. dig. prof. proximal to carpals	TIP distal phalanx
	Superficial Head	
Flexor pollicis brevis	Retinaculum and trapezium	Both heads on proximal phalanx
	Deep Head	
	Flexor retinaculum and trapezoid	To head of metacarpal
Abductor brevis	Flexor retinaculum, tubercle of scaphoid, crest trapezium	Lateral base of proximal phalanx; fibers into dorsal expansion
	Transverse Head	
Adductor pollicis	Palmar surface meta 3 Heads quite distinct	Meta head to base first phal.
	Oblique Head	
	Base of meta 2 and 3 and capitate.	Meta head into fibers of transverse.
Abductor pollicis longus	Rad. to ulna. as one with ext. brev.	To ses. and trapezium, as one with ext. brev.

Table 17 (cont'd.)

Muscle	Origin	Insertion
M.mulatta		
Extensor pollicis brevis	rad. to ulna. as one with abd. longus	base of the metacarpal. Tendon sep. from abd. longus, but inserting as one.
Extensor pollicis longus	Post. aspect ulna. and adjacent interos memb. distal to abd. longus	Base of the distal phal.
Opponens pollicis	Same as Papio	Head of the metacarpal, towards the lateral aspect
Flexor pollicis longus	Superficial aspect flex. dig. prof. At carpals.	TIP distal phalanx
	Superficial Head	
Flexor pollicis brevis	Retinaculum and trapezium	Both heads on proximal phalanx
	Deep Head	
	Flexor retinaculum and trapezoid	To head of metacarpal
Abductor brevis	Flexor retinaculum, tubercle of scaphoid, crest trapezium	Lateral base of proximal phalanx; fibers into dorsal expansion
	Transverse Head	
Adductor pollicis	Palmar surface meta 3 Heads quite distinct	On metacarpal shaft, lower, (proximal) to insertion of oblique.
	Oblique Head	
	Base of meta 2 and 3, and capitate	Ses. behind MCP joint and base first phal.
Abductor pollicis longus	Rad. to ulna. as one with ext. brev.; some specimens separate	To sesamoid and trapezium. Sep. tendon from ext. brev. but inserting as one.

Table 17 (cont'd.)

Muscle	Origin	Insertion
C.aethiops		
Extensor pollicis brevis	On ul., near ol. proc. & adjacent interos. mem. where joins abd. but distal to abd.	Crosses over on top abd. tend. to insert on trap, meta, ses. Tend. begins as free 1/3 down from orig. fibers to meta
Extensor pollicis longus	Post. aspect ul. & interos.mem. prox. to orig. abd. poll. long.	Base terminal phalanx
Opponens pollicis	Retinac. & ridge trap. & scaph.	Medial-lat head meta. palmar
Flexor pollicis longus	Superficial aspect flex. dig. profundus distal to carpals, i.e. at palm	TIP terminal phalanx
Flexor pollicis brevis	Retinaculum & ridge trapezium	Lat. base prox. phal. & head meta.
Abductor brevis	Ses. & retin. & ridge trap.	Prox. phal by tend. visible on lat-dorsal
Adductor pollicis		
Transverse	Palmar surf. 3rd meta. across d2	Head meta., base phal.
Oblique	Base d2	
Abductor pollicis longus	Post. aspect rad. & interos. mem. to ul. prox. to ext. brev.	Base meta. fibers to ses. on trap.
E.patas		
Extensor pollicis brevis	Post. aspect ul. & adj. interos. mem. is larger m. than abd. & joins abd. in interos. O.distal to abd.	On ses. But one slip of ext. tend. attaches to meta. lat. & dist. to I. of abd.
Extensor pollicis longus	Post. aspect ul. & interos. mem. prox. orig. abd. poll. long.	Base terminal phal.

Table 17 (cont'd.)

Muscle	Origin	Insertion
Opponens pollicis	Retinac. & ridge trap and scaph.	Medial-lat. head meta. palmar
Flexor pollicis longus	Same as C.aethiops, but joins flex. dig. prof. at carpals	TIP terminal phalanx
Flexor pollicis brevis	Retinaculum & ridge trapezium	Phal. & Joins inserting fibers of abd.brev. with fibers attaching to head meta.
Abductor pollicis brevis	Retinac & ses & scaphoid	Slightly more dist. and lat. on base prox. phal. than flexor.
Adductor pollicis Transverse	Palmar surf. d2 and d3	Head meta to head phal on lat. as m. fibers in conn.tissue
Oblique	Base d2	
Abductor pollicis longus	Same as C.aethiops. Thin tend. begins 1/3 from origin.	Base meta with 2nd tend. joining tend. of ext & attaching ses. NO trap.
<u>C.neglectus</u>		
Extensor pollicis brevis	On ul. etc. separ. tend. slightly above carpals	On ses. & ret. & base meta.
Extensor pollicis longus	Post.aspect ul. & interos. mem. prox. orig. abd. poll. long.	Base terminal phal.
Opponens pollicis	Same as E.patas & receives tend. from abd. ext. complex.	Same as E.patas but bunched at base, thin tendon to I.
Flexor pollicis longus	Same as C.aethiops	Same as C.aethiops
Flexor pollicis brevis	Same as E.patas and joined with opponens	Head meta. to base phal. crosses meta diagonally.

Table 17 (cont'd.)

Muscle	Origin	Insertion
Abductor brevis	Same as E.patas	Lat. head meta.
Adductor pollicis		
Transverse	Head d2 and d3	Same as E.patas
Oblique	Same as E.patas	
Abductor pollicis longus	Same as E.patas	One slip to trap. Major slip to base meta. etc. Into opp. poll.
C.mitis		
Extensor pollicis brevis	As one with abd. from rad. to ul.	As one with abd. to ses & base meta. impossible to disting. sep. slip.
Extensor pollicis longus	Post.aspect ul. & interos. mem. prox to orig. abd-ext Extra piece from ext. dig. prof.	Same as E.patas.
Opponens pollicis	Like C.aethiops.	Head meta. lateral
Flexor pollicis longus	Same as C.aethiops	Same as C.aethiops
Flexor pollicis brevis	Like C.aethiops	Base phal. & head meta
Abductor brevis	Retina. & ridge trap.	Base prox. phal. lat.
Adductor pollicis		
Transverse	Same as C.neglectus	Lat. head meta. some fibers to phal.
Oblique	Same as C.neglectus	
Abductor pollicis longus	Rad. to ul. one with ext. brev. tend. is visible but not separable.	See I.ext. brev. Also inserts trap.
Colobus Abyssinicus		
Extensor pollicis brevis	Same as C.mitis	Muscle to carpals where emerges as tend. one with abd. fibers can be demarcated but absolutely united, & I.ses & meta

Table 17 (cont'd.)

Muscle	Origin	Insertion
Abductor brevis	Unknown	Base phal. medial & distal to flexor
Adductor pollicis		
Transverse	Base meta lateral of d4	From base to almost head phal.
Oblique	Capitate, base d2 & d3, extra bit from base d5 lateral into oblique at palm d3.	
Abductor pollicis longus	Rad. to ul. tendon visible 1/3 from olec. but immersed in m. fiber.	Inserts as one with ext. brev. Meta and ses. & trap.

CHAPTER V. DISCUSSION

None of the species studied was observed to approach 100% in frequency of Refined-Opposition use with food items of small size and smooth texture. The statement that opposition is intrinsic to the Cercopithecid hand (Schultz, 1926; Napier, 1966; Campbell, 1966, 1968) therefore, requires qualification.

All of these species have the same number of pollical muscles and carpals. Where the pattern of origin or insertion of the muscles and the articulation of the carpals was the same for all species, that pattern was taken as an absolute limitation on opposition. These factors include: (1) the insertion of the flexor pollicis longus; and (2) the insertion of the abductor pollicis longus - extensor pollicis brevis complex.

For all species studied, the flexor pollicis longus inserted at the distal end of the distal phalanx. As its antagonist, the extensor pollicis longus inserted at the base of the distal phalanx, there cannot be counterforce exerted against its action.

Clinical studies of Homo sapiens have shown that such a pattern results in loss of stability of the interphalangeal joint, and consequent loss of control of the digit in precision grips (Kaplan, 1953). This observation reinforces the view that the distal insertion of the flexor pollicis longus inclines the species studied to press the terminal phalanx of the pollex against the side of the second digit where stability at the interphalangeal joint is enhanced.

The abductor pollicis longus-extensor pollicis brevis complex inserted in all Cercopithecinae on the base of the metacarpal, the trapezium and the sesamoid.

In _Homo sapiens_, not only does the complex consist of two independent muscles from origin to insertion, but insertion extends more distally on the pollex, the abductor inserting on the metacarpal and the extensor onto the proximal phalanx. The proximal insertion of the complex in Cercopithecinae seems to make it function as an extensor ossis metacarpal pollicis or supinator manus, so that working across the carpometacarpal joint the digit is pulled dorsad, and is only slightly abducted. Furthermore, extension of the digit occurs primarily at the distal phalanx, with some action across the carpometacarpal joint, but not over the metacarpophalangeal joint, and abduction is basically limited to the activity of the abductor pollicis brevis.

As abduction is a primary movement in the total act of opposition, its decrease through the absence of a functional abductor longus limits the ability to oppose. This fact has been confirmed for _Homo sapiens_ in clinical studies (Napier, 1952).

Variation in observed manipulative behavior of the several species of Cercopithecinae suggests anatomical differences between them. Those osteological and myological factors which were observed to vary between species are judged to be the critical variables. These include: (1) the origin of the flexor pollicis longus, (2) the insertion of the abductor - extensor complex, (3) the curvature of the carpal canal, and (4) the transverse head of the adductor.

The origin of the flexor pollicis longus varied in degrees of independence from the flexor digitorum profundus. It originated at the carpals, proximal to the carpals, or distal to the carpals. As those species with highest R-O performance had the most proximal origin of the flexor pollicis longus (P.doguera, M.mulatta, E.patas), it was deduced that the greater resulting length of the flexor permitted greater independence in flexion of the pollex from the other digits. The greater independence would permit manipulation in relation to the other digits (as in opposition) rather than synergistically with the other digits.

The intimate relation of the abductor to the extensor in a muscular complex results in its acting as an extensor of the metacarpal or supinator of the hand, as noted above. However, the degree of independence of the abductor longus from the extensor brevis at origin and insertion varied between species. The greater the independence, the higher the frequency of Refined-Opposition. With insertion on the

Table 18

Summary of Variables Influencing Opposition

	Colobus	C. mitis	C. neglectus	C. aethiops	M. mulatta	E. patas	P. doguera	H. sapiens
Refined-Opposition Performance	0	1	4	4	6	6	9	10
Carpal Canal	3	3	4	4	6	6	8	10
Styloid Process Metacarpalis Ulnar	0	0	1	1	7	7	7	10
Abductor Extensor are Separate at Origin	0	0	8	8	0 or 7	8	0	10
Abd. Ext. are Separable at Insertion	0	0	7	7	7	9	1	10
FPL Inserts TIP Distal Phalanx	10	10	10	10	10	10	10	0
FPL Originates at Carpals or More Proximal	0	3	3	3	5	5	6	10
Adductor Transversus is Weaker than Oblique	0	0	8	8	7	9	7	6

Tree to Ground Gradient Arbitrary Evaluation 0-10 metacarpal and fibers anchored on the sesamoid and/or trapezium, contraction principally results in motion dorsad, but mediated by the more volar fibers, some abduction is permitted.

Degree of independence correlated with manipulative behavior except in _Papio doguera_ subjects where the muscular configuration of the complex was more like the species with lower frequency counts of R-O. Although even here, while the origin and insertion of the two muscle entities were as one mass, the tendon was separable at the carpals before intertwining at insertion. Significantly, _Papio doguera_ has the greatest degree of Passive Opposition. As it is the complex of variables and not a single factor which must account for manipulative behavior, perhaps the fact that the distance between the pollex and the second digit is reduced due to the curvature of the carpus, compensates for the configuration of the abductor-extensor complex in this species.

The curvature of the carpal canal, resulting in Passive Opposition, significantly corresponded to observed use of the hand. The greatest curvature occurred in _Papio doguera_, and decreased through a gradient that runs from _M.mulatta_ to _E.patas_ to _C.aethiops_, _C.neglectus_ and _C.mitis_. In this last species, the curvature is negligible, and the trapezium and trapezoid lie level to each other. The consequence of this is that the muscles must compensate for the greater distance through the arc of rotation between the pad of the distal phalanx of the pollex and the distal phalanx of the second digit. Since the muscles, due to their positions, as noted earlier, cannot compensate, opposition is effectively decreased. This decrease in ability to oppose was reflected in the low frequency of R-O.

The adductor pollicis functions in opposition to stabilize the metacarpophalangeal joint (Napier, 1966). It works as well, as the antagonist to the abductor-extensor complex (Wood-Jones, 1920), drawing the pollex medially towards the second digit. The transverse head was considerably thinner - even to the point of appearing as fibers only - in those species with highest Refined-Opposition performance. This fact suggests that in these species (P. doguera, M.mulatta, E.patas, C.aethiops, C.neglectus), stability of the metacarpophalangeal joint is maintained by the oblique head, but the action of drawing the thumb medially is reduced. In species deriving a small degree of abduction from the abductor longus, as in all the species studied, a weak transverse head facilitates abduction by reducing counterforce, thus permitting greater opposition (Table 18).

Refined-Opposition in the species of Cercopithecinae studied depends on the abductor brevis and opponens pollicis. The other pollical muscles, which enhance opposition in other species of Primates (i.e., H.sapiens), are limiting factors in these species. Frequency of Refined-Opposition coincides with habitat and diet. Those species which inhabit savanna and which subsist principally on seeds and grasses (E.patas, P.doguera), have the highest frequency count of Refined-Opposition grip. Species with more varied habitat, i.e., C.aethiops and M.mulatta, which occupy savanna or marginal forests, tend to be intermediate between the committed tree dwellers and committed savanna dwellers in terms of the anatomical variables and frequency counts.

The gallery forest dwellers, who occasionally descend to the substrate (C.neglectus), are similar to the committed ground dwellers in certain anatomical features, particularly the abductor-extensor complex and the transverse head of the adductor. This is reflected in the R-O performance. However, the data concerning their feeding habits are largely anecdotal, and the degree to which they exploit the food resources of the substrate must await future reports. On the basis of their manipulative behavior and anatomy, a prediction is warranted that some of the foods on which they depend will be like that of C.aethiops or E.patas, i.e., seeds, grasses or the like.

The diet of tree dwellers (C.ascanius and C.mitis), comprises food items that can be handled with grips of the whole hand (fruits), such as the CUP or just the digits d2-d4 (leaves) as in the N-O grip. The high Quasi-Opposition frequency observed on food items such as grain, coincides with the field reports of diets which lack similar food items.

The non-human primate hand has a dual function: one is manipulation, the other locomotion. While it may be true for Prosimii and Pongidae that the hand has adapted for locomotion and that its manipulative abilities are a result of the locomotor adaptation (Jolly, 1964; Tuttle, 1967), the fact that the Cercopithecine hand is generalized (Midlo, 1934; Romer, 1966), permits a more particular adaptation for acts of manipulation.

The three types of data analyzed: behavioral, anatomical and ecological, correlate. The lack of locomotor specialization in the Cercopithecine hand suggests that habitat may have been a factor selecting for the structures now present. The habitat permits the growth of certain foods, and the dependence on these nutrients would favor structural adaptation.

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I was born in France in 1939 and became a citizen of the United States in 1947. I received my Bachelor's Degree in 1960 from New York University and my Masters Degree in Anthropology in 1962 from the same institution.

After having taught a core curriculum in Anthropology at a private school in New York City for five years, I left for Kenya where I did research on Cercopithecinae. My principal research interest is in the physiological and anatomical correlates of behavior in Old World monkeys.

While working for the doctorate in Anthropology at the Graduate Center of the City University of New York, I was a lecturer at Hunter College and presently hold an appointment as Assistant Professor of Physical Anthropology at Toronto University, beginning September, 1969.