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AN ELUCIDATION OF THE ARBOREAL THEORY OF PRIMATE EVOLUTION: A BEHAVIORAL COMPARISON OF THE MANUS OF THE SQUIRREL MONKEY, THE TREE SHREW, AND THE GREY SQUIRREL

by

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VITA

The author, Catherine Anne Walla-Murphy, is the daughter of Louis B. Walla and Mary L. (Mc Garvey) Walla. She was born October 18, 1948, in Chicago, Illinois.

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CHAPTER I

THE PROBLEM

Taxonomy orders animals, including primates, in an ecologically significant way since taxonomic groupings develop from ancestors which evolved into a rather specific type of ecological niche (Mayr, 1968; Birdsell, 1972). The common basis for differentiating the order of primates from other zoological taxonomic orders is a number of discrete traits which relate the order to the general ecological habitat of the primates. This is exemplified by Le Gros Clark (1959: 43) when he listed the primate characteristics as:

1. preservation of a general structure of limbs with a primitive pentadactyly, and the retention of certain elements of the limb skeleton which tend to be reduced or to disappear in some groups of mammals;
2. an enhancement of the free mobility of the digits, especially the thumb and the big toe;
3. the replacement of the sharp compressed claws by flattened nails associated with the development or highly sensitive tactile pads on the digits;
4. the progressive abbreviation of the snout or muzzle;
5. the elaboration and perfection of the visual apparatus with the development to varying degrees of binocular vision;
6. the reduction of the apparatus of smell;
7. the loss of certain elements of primitive mammalian dentition and the preservation of a simple cusp pattern of the molar teeth;

8. progressive expansions and elaboration of the brain affecting predominantly the cerebral cortex and its dependencies; and
9. progressive and increasing effective development of those gestational processes concerned with the nourishment of the fetus before birth.

These features recognize that the primate order is characterized by a relative lack of specialization when compared with the extreme specializations of most other mammalian orders. Other physical anthropologists who have incorporated these features in their definitions of the order of primates include Brace and Montagu (1965), Campbell (1966), and Hulse (1971). They, along with Le Gros Clark (1959, 1968), attribute this retention of primitive mammalian traits, that is, the lack of specialization, to the primate order's arboreal habit. "Since from the outset of their evolutionary origin from the arboreal mammalian prototype, the primates remained in the trees, and preserved these advantageous, though primitive anatomical characters" (Le Gros Clark, 1968: 6).

The idea that an arboreal habitat supplied the environmental pressures that determined the distinctive characteristics of the primates has historical support in Matthew's hypothesis (1904) which states that the earliest of mammals were small arboreal animals. He proposed eleven traits which he claimed were widespread among the earliest of mammals: small size; bunadont molars; flexibly articulated cervical and lumbar vertebrae; a long, powerful, thick based (i.e., presumably prehensile) tail; unreduced clavicles; narrow and rodlike ilia; non-cursorial limbs with long proximal and short distal segments; an unreduced radius capable of being supinated; flexible wrists and ankles; pentadactyl cheridia, and a "more or less opposable" pollex. Matthews considered the primates to have retained these primitive mammalian characteristics to a greater extent than any of the other mammals. The value of this hypothesis is that if the arboreal habits are primitive, this is important in any reconstruction of the selective pressures that govern primate phylogeny since it determines whether the traits evolved simply as a result of inheritance or whether they evolved simply as a result of environmental pressures (Cartmill, 1970).

Smith (1924), in an address to the British Association for the Advancement of Science in 1912 explained the origin and persistance of many of the primate evolutionary trends (such as the reduction of olfaction, an enlargement of the brain, visual field overlap, and grasping specializations of the cheiridia) by assuming that the Mesozoic primate ancestors had initiated arboreal habits. F. Wood Jones (1926) supported Smith's hypothesis of the primitive ancestry of the primate arboreal habit. He stated:

> An amphibian or unspecialized reptile ascends an obstacle by clambering up, its feet are applied to the surface of the obstacle up which it clambers. It makes no attempt to obtain a grip by nails or claws, but it trusts merely to the opposition of its feet to the

> surface to which it clings. Two points must be especially noted. As it progresses, it repeatedly reaches ahead with one or another of its forelimbs for a new hold, and whilst doing this its body weight is temporarily thrown upon its hindlimbs. And again, in reaching out its forelimb, the freedom of rotation possessed by the second segment of the limb allows the animal to apply the palmar surface of its hand against any new hold which may present itself at almost any angle. As arboreal life becomes more complete the search for a new foothold will become a far more exacting business then it is in the mere clambering we have pictured. The more exacting this search becomes, the more will there tend to develop the most important factor -- the specialization of the functions of the fore- and hindlimbs. While the animal reaches about with its forelimbs, the hindlimb becomes the supporting organ. With the evolution of the forelimbs from any servile function as supporting the weight of the body; it becomes a free organ full of possibilities, and already capable of many things (Jones, 1926: 16-17).

Thus Jones' theory suggests that the selection for tree climbing formed the differential use of the fore- and hindlimbs; the forelimbs are employed to grasp the substrate, while the hindlimbs are employed to support the animal and to propel the body forward. This differentiation of the limbs, which developed to its greatest extent in the primate order, furthered the development of other primate characteristics such as the reduction of the olfactory sense, the snout, and the whole facial skeleton. Jones indicated that once the hands of the animal were able to function as grasping and manipulating organs, the snout was no longer needed as a tactile organ. "In the primates, owing to the preponderant use of the forelimb, there is no need for a mouth which reaches out for food, or for a mouth which seizes foods or kills it when seized, all these functions being discharged by the mobile and grasping forelimb" (Jones, 1926: 87). Further, as the snout dwindled, the eyes were turned to the front of the face, and the head was so positioned to permit the animal to shake its head sideways and up and down. The liberation of the forelimbs also can be seen as the beginning of a trend leading towards upright posture. Jones' theory further professed that an arboreal habitat had influenced the primates' reproductive system:

> . . .larger litters are, as a rule, produced among animals living such a life as affords rest and protection for the female during pregnancy. Pregnancy with a large litter and active arboreal life are almost incompatible. Helpless offspring in large numbers may be managed and cared for in some safe terrestrial nursery, but up a tree even where large numbers of such offspring are born, it is doubtful if very many would survive. But nest building is only a temporary expedient in mammalian evolution and reduction of the number of young produced at a birth is the ultimate outcome in a truly arboreal life (Jones, 1926: 138).

The major objection (Howells, 1947) to Jones' "arboreal theory of primates" was that there are at least nine other orders of mammals which are arboreal in their habitat. The question was often raised by the objectors of this theory was why the arboreal selective pressures did not affect these other arboreal mammals and produce in them such characteristics as the reduction of the snout and the olfactory sense, convergent eye orbitals, an enlargement of the brain, greater manipulatory functions of the cheiridia, etc. Jones (1926) seemed to answer this question in stating that the other mammalian orders, some time during their phylogenetic history, descended from the trees and lived in a terrestrial environment for some period and thereby lost many of the arboreal characteristics.

> Other mammalian stocks have taken to an arboreal habit, but they have taken to it after varied periods of quadrupedal life. They have taken to it too late to derive the full benefits from it, for they took to it with the forelimbs already deprived of some of their inherited mobility. Such animals never become perfect tree climbers. They may acquire an extra ordinary skill in running about the branches of trees (such as the rodents) but in this climbing the grip is not obtained by the application of the palmar surface of the hand, but by the hook-like action of the claws and nails. . . (Jones, 1926: 18).

Le Gros Clark (1959) reformulated Jones' theory of arboreality with the acceptance of the students of primate evolution for some time. He proposed that the tree shrews (tupaiidae) are persistently primitive lemuroids that have somehow failed to develop the perfected adaptations to arboreal life seen in other extant primates. Le Gros Clark believed that the primitive insectivores were arboreal animals with clawed, nonprehensile hands and feet, small eyes and brains, and elaborate olfactory apparatus. The unspecialized, squirrel-like climbing habit of tree shrews (and the ancestral primates) is used by Le Gros Clark to explain their primate-like morphology.

Napier and Napier (1967: 15) modified Jones' arboreal history to the extent that the primates had adapted to a specialized arboreal habitat which has been shared with none of the other nine orders of arboreal mammals. Cartmill (1970, 1972, 1974a) expanded the theme of a specialized arboreal habitat to account for the characteristics of the primates in his restatement of the arboreal theory:

> The difference of the primates from the other placental mammals is a result of gradual adaptation for visually guided manual predation on insect prey among terminal branches, a way of life characterized by. . . visualfield overlap (with attendant cranial neurological modification) and grasping specializations of the cheiridia which are primary adaptations to this habitus and. . .the primate trends towards enclosure of the orbits, regression of the olfactory apparatus, and recession of the rostrum are explicable as secondary effects of the progressive perfection of these primary adaptations (Cartmill, 1970: 425).

Thus, Cartmill's revised arboreal theory is based on the premise that primates evolved to their present form as the result of an adaptation for visually guided manual predation of insect prey among terminal branches.

Four studies may be applied to test the validity of either the original arboreal theory (which hypothesizes) that the primates' characteristics are an adaptation to a specialized arboreal habitat; i.e., a fine terminal branch habitat). These studies may then be used to differentiate the original from the revised arboreal theory. The first study is to describe the basal primate stock and its characteristics and compare it to other basal stocks of other arboreal mammals; the second study is to demonstrate that the present primate characteristics have evolved in an arboreal habitat; the third study is a demonstration of the exact habitat of the primates to show that the primate trends are due to either a specialized arboreal habitat or just an arboreal habitat per se; the fourth study is to demonstrate the difference which exists between the primates and other arboreal mammals and explain the reason for this differentiation.

This thesis will adapt a comparative strategy to partially test the original and the revised theory of primates in so far as the adaptations of the manus is concerned. It will focus upon the key differences of the manus of a primate, the squirrel monkey (Saimiri sciurius) and two other arboreal animals, the tree shrew (Tupaia glis) and the grey squirrel (Sciurus carolinensis) which may be attributed to differences in their specific ecological adaptations. The squirrel monkey and the grey squirrel have been chosen as models for this study because of the similarities of the size, shape and similarities of arboreality. The tree shrew has been chosen as the third model because of its frequent reference as a model of a primitive primate which is considered as a transition between the early mammals and primates.

To evaluate the arboreal theory, the following studies will be conducted in the succeeding chapters. Chapter two, a summary of the paleontological history of the squirrel monkey, the tree shrew and the grey squirrel, provides the possible evolutionary background (possible, in that the present knowledge of the paleontological history is limited) for the description of the function of the manus which is to follow. Chapter three compares the paleo- and present ecological habitat of the animals. Chapter four contains a physical and behavioral description of the experimental animals. Chapter five reports the experimental procedures which have been conducted on the squirrel monkey in order to test: (1) the animal's proficiency of locomotion on various sized branches positioned at a 45° angle, (2) the animal's manual dexterity in maneuvering and manipulating objects and (3) the animal's variance of the grasp of its hands. The experimental section compares the above data with similar data collected by Bishop (1964) on tree shrews. (Squirrels have not been tested in these experiments due to the lack of adequate caging and testing facilities.)

CHAPTER II

PALEONTOLOGICAL HISTORY OF THE SQUIRREL MONKEY, THE TREE SHREW, AND THE GREY SQUIRREL

In testing the arboreal theory of primates it is important to demonstrate whether or not specific primate characteristics are an enhancement of characteristics possessed by the basal mammalian stock or by later basal primate stock. Further, characteristics of the basal primate stock should be compared with those of other basal stocks of arboreal mammals (specifically for this example the basal insectivore and rodent stocks) to indicate the similarities and differences between the stocks.

In tracing the lineages of the squirrel monkey, the tree shrew, and the squirrel, it should be noted that all evidence is based on paleontological remains which are extremely fragmentary. This limitation does not appear to be due to the small size and fragility of these animals, however, since other small-animal remains are found in abundance in some areas. Rather, it appears that it is the animals' arboreal habits which keep them away from the usual sites of deposition (Shotwell, 1955).

Basal Mammalian Stock

During the late Paleozoic and earliest Mesozoic times (Table 1), a reptilian stock, the synapsids, existed. These animals were the apparent common ancestors from which both the dinosaurs and mammals evolved. The first mammal-like representative, the pelycosaurs, were found in the Late Carboniferous. They still resembled to a great degree, however, the primitive reptiles, the therapsids, which were more mammal-like. The therapsids radiated radically from the main pelycosaur line later in the Permian (Romer, 1971). The therapsids were intermediates between the reptilian lines, still possessing the sprawling reptilian limbs, yet having body proportions which led to the beginning of a heat conservation mechanism which is so important to modern day mammals (Bakker, 1971). The therapsids flourished until the Triassic when their population dwindled, apparently due to the rise of the large ruling reptiles, the archosaurs (better known as the dinosaurs). The mammal-like reptiles disappeared from the fossil records due to the dinosaurs' dominance. Their descendants, the earliest mammals, had survived for 180 million years. They did so, however, only as small and inconspicuous forms (Birdsell, 1972). The early mammals survived because they were able to produce their own body heat and conserve it with their insulating fur. It appears they lacked, however, an efficient cooling

TABLE 1

STANDARD GEOLOGICAL TABLE

CENOZOIC ERE (65 million years to Present)

Quaternary	Pleistocene	3 million years to present
Tertiary	Pliocene	12 - 3 million years
	Miocene	25 - 12 million years
	Oligocene	34 - 25 million years
	Eocene	58 - 34 million years
	Paleocene	65 - 58 million years

MESOZOIC ERA (235 - 65 million years)

Cretaceous

Jurassic

Triassic

PALEOZOIC ERA (600 - 235 million years)

Permian

Upper Carboniferous

Lower Carboniferous

Devonian

Silurian

Ordovician

Cambrian

CIRCA (5,000 to 600 million years)

NOTE: This table has been modified after table presented in Butzer (1971) and Simons (1972) system. What this may indicate is that the early mammals were able to produce enough heat to raise their body temperature to enable them to carry on nocturnal foraging. During the day, however, due to an inefficient evaporation system, the early mammals were forced to seek shelter from the midday sun. Because of their small size, they were able to protect themselves from the dinosaurs by finding small protective shelters in trees or burrows in the ground which were unavailable to the large, lumbering dinosaurs (Bakker, 1971). It appears that the dinosaurs, who may possibly have been endothermic (and therefore were able to sustain the climatic shifts of the Cretaceous) fell because of their inability to adapt to a changing topography. At the end of the Cretaceous, there occurred a draining of the shallow seas on the continents and a lull in mountain building activity in most parts of the world. Such geological events decreased the variety of habitats that were available to land animals, and thus increased competition. They could also have caused the collapse of intricate, highly involved ecosystems. The larger animals, such as the dinosaurs, seemed to be more affected than the smaller ones (Bakker, 1975). Following the demise of the ruling reptiles, most of the mammals were able to develop a more diurnal habitat.

The question of whether the early mammals were arboreal or terrestrial according to their habitat has been answered by Haines (1958), who has further been supported by Simons (1972). Haines states that it appears that the specializations of the hands and feet which are characteristic of many arboreal mammals cannot be recognized in the skeletal remains of the early placental mammals. It seems more probable from these remains that they were terrestrial in habitat.

Paleontological Ancestry of the Squirrel Monkey

The earliest known probable primate was described by Van Valen and Sloan (1965). This specimen was found in the United States in Montana. The genus *Purgatorius* (placed under the suborder of Prosimians) which is known only by the remains of about a dozen isolated teeth, is believed to have lived in the late Cretaceous and early Paleocene. Since its characteristics indicates that it may have a close relationship to the insectivores, it has been suggested that at this point in time, it is close to the period when the primates became differentiated from the basal mammalian placental stock (Kurten, 1972). However, Van Valen and Sloan (1965) do not consider *Purgatorius* to be the probable candidate of the stem primates.

The Plesiadapidae, remains which have been found in both Europe and North America, was one of the most successful Paleocene families of primates, both in number of known species as well as in the number of individual fossils found (Szalay, 1972; Mc Kenna, 1966). Pronothodectes, the oldest genus of Plesiadapidae, was found in the middle Paleocene deposits of Montana and New Mexico. It is considered by Simons, (1967, 1972) to be near the basal ancestry of the family of Plesiadapidae from which later species evolved.

The best known specimens of the family Plesiadapidae are from the genus Plesiadapis, a specialized lemur-like prosimian known from both Europe and North America (Simons, 1968). In appearance, Plesiadapis was rather rodent-like having the gliriform adaptation of a pair of gnawing incisors followed by a diastema before the cheek teeth (Romer, 1966). On its hands, rather than having nails, it had long, arched claws which were flattened from side to side. Its fore- and hindlimbs were of nearly equal length; and its general size was that of the various species of squirrels, the smallest being about the size of the grey squirrel. Plesiadapis is visualized as being a rather generalized mammal with a large, long snout, laterally directed orbits, a horizontally oriented head with the foramen magnum directed entirely to the rear and a small brain case (Simons, 1963, 1967). On the basis of its molar teeth, it is considered to be not far removed horizontally from the ancestral stock of the primates even though it possesses this rodent-like appearance (Van Valen, 1965).

Generally, from examination of the dentition, it appears that the Paleocene families of primates fed predominantly on vegetation. Szalay (1972) postulates from the molar patterns of this dentition that the earliest primates' teeth were not adapted for eating muscle fibers of meat. Rather, the dentition indicates that they were adapted to a herbivorous-frugivorous diet. Correlating this diet with the tropical angiosperm forest conditions of the Paleocene in Europe and North America it may be considered that these primates were arboreal since in the tropical forests fruit, seed and leaf eating activities often occur away from the ground. This supposition is supported by Simons (1967, 1972) on the basis of skeletal remains of Plesiadapis which indicate that the locomotion of these primates may have resembled that of the grey squirrel. The claws found on the fossil remains indicate an adaptation for quadrupedal scrambling up the bark of large trees. The forelimbs were massive and seem to have been adapted for extreme flexion.

The subfamily Omomyinae, which is totally extinct (as are the plesiadapids), was widespread in China, Europe, and North America. The omomyids were first found in Paleocene remains, however, they became most diversified throughout the Eocene. The radiation of these prosimians occurred approximately from 55 to 44 million years ago. The omomyids are related to the tarsioids (Mc Kenna, 1967). Simons (1963, 1967, 1968, 1969, 1972), Mc Kenna (1967), Gazin (1958), Patterson and Pascual (1968), and Van Valen (1969) have speculated that the omomyids were the ancestors of the Ceboidea. Simons (1963, 1967, 1968, 1969, 1972) has also speculated that within the omomyid subfamily, there could be found the common ancestor of the Anthropoidea, that is; the Ceboidea, the Cercopithecoidea, and the Hominoidea. Simons, however, bases his postulation on dental evidence only. Simons (1968, 1972) and Van Valen (1969) consider the omomyid Rooneyia to be the likely candidate for the ancestor to the Neotropical (South American monkeys[1]). Rooneyia was found in deposits in Texas dating to about 35 million years ago. The fossil remains include one of the most complete fossil primate skulls known from the New World. The position of the foramen magnum suggests that Rooneyia possessed a locomotor form that was more of a hopping form than a quadruped. A study of a natural endocranial cast of the skull suggest that the brain of Rooneyia had a highly

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[1] Wilson (1966) denies that Rooneyia could be a possible ancestor for the Ceboidea on the basis of the number of teeth found related to the fossil. He does suggest that Rooneyia, however, may be a possible candidate as an ancestor for the Old World monkeys.

developed visual system and small olfactory bulbs. The animal appeared to have a brain approaching a level of early primate rather than prosimian development (Simons, 1972).

Other Eocene omomyids also appear to have some relation to the ancestry of the Ceboidea. Gazin (1958) considers the omomyine prosimian, Washakius, to be near the source of the neotropical monkeys. This prosimian was found in middle Eocene deposits in Wyoming. Through analysis of the structure and size of its teeth, it appears that Washakius was moving towards an adaptation to a strict herbivorous diet. While the structure of such dentition is common in ungulates, it is almost never seen among primates (Simons, 1972).

Another omomyine prosimian thought to be related to the Ceboidea is Macrotarsius found in Montana in lower Oligocene deposits. It is also through the animals' dental structure that it resembles the Neotropical monkeys (Simons, 1972).

Only three genera of the Paleocene-Eocene primates survived into the Oligocene in North America: Rooneyia, Macrotarsius, and Ekgnowechashala. The last of these survived only into the late Oligocene (Simons, 1972).

It is interesting to note that from the end of the Eocene to the present time the mean annual temperature in North America has been constantly declining. None of the primates, except for langurs, macques, and humans, have been able to adapt to a non-temperate environment, partially because of the limiting factor of temperature but mostly to the unavailability of food in the winter (Napier & Napier, 1967). It appears that temperature is an even greater limiting factor to the platyrrhines as opposed to the catarrhines. It could be postulated, therefore, that with the reduction of the mean annual temperature due to a worldwide cooling trend there also occurred a reduction of living space, i.e., the tropical rain forest, for the primates.

Primates in the last Eocene and the Oligocene in North America, therefore, had three opportunities open to them: (1) remain in the same area and adapt to the changing environmental conditions; if not, (2) become extinct; or, (3) migrate south and follow the declining tropical forest. Since no primates have yet been found in North America later than the late Oligocene-early Miocene deposits, the first of these choices may be eliminated. And since the Eocene-Oligocene nearctic (North American) primates are probably ancestral to the Ceboidea (however, an African ancestry has been suggested, see page 23) it is reasonable to assume that the New World primates did not become extinct. Therefore, only a third possibility is left open, which is that the primates migrated southwards as their tropical environment declined southward.

In general, the number of fossils represented in South America are relatively few. To date, there have only been nine individual fossil primates found in the neotropical region. According to Simons (1972), the present fossil evidence indicates that the primates reached South America sometime in the early Oligocene.

The oldest primate known in South America, *Branisella*, was located in Bolivia. According to Simons' analysis (1972) of the dentition of this fossil, it appears to resemble *Saimiri*, the squirrel monkey. The second oldest fossil found in South America, *Dolichocebus*, was located in deposits ranging from the late Oligocene. The remains of this find are primarily a crushed and distorted cranium which tends to characterize the animal as having a rather long skull. Simons attributes this dolichocephalic condition possibly to a distortion of the skull during fossilization. However, there is the possibility that this animal possessed the ceboid trend towards a large, long brain case as especially noted in *Saimiri*.

Neosaimiri fieldsi is a late Miocene primate found in Colombia. The fossil finds of this animal is represented by part of a mandible with most of its teeth set into it. Stirton's analysis (1951) of this material reveals that both the size and morphology of the dentition relegate this fossil primate near to the ancestry of modern *Saimiri*.

The fossil record of primates from the Pliocene in South America is left blank until fossils identical to the modern monkeys are identified (Simons, 1963).

The basic questions relating to all of the fossil finds in the neotropical region are: why there is no evidence of primates before the early Oligocene and where was the province of those primates which have been found. As stated above, it appears that the neotropical primates evolved from the nearctic primates. However, geological evidence indicates that South America together with part of Central America was isolated from North America throughout most of the Cenozoic, probably from the early Paleocene to the late Pliocene by a Pacific-Atlantic marine connection. The Central American Panamanian land bridge which now connects the two continents arose only about two to three million years ago (Napier, 1970a, 1970b; Fittkau, 1969; Simpson, 1965, 1969; Patterson & Pascual, 1968; Romer, 1966; and Darlington, 1957). If in fact the neotropical primates evolved from the nearctic omomyids, then it must be questioned as to how these animals crossed from one continent to the other across a rather extensive marine barrier.

Simpson (1965) in describing the early neotropical fossil primates as the "old island hoppers" indicated that entry of the nearctic primates into South America was by waif dispersal. Geological findings, Simpson relates, give evidence that during the late Eocene and early Oligocene there was a series of islands between North and South America. The seaways would bar any extensive interchange of animals between the two continents, but the islands would facilitate the overseas spread of a few special groups of small animals in what Simpson termed a "sweepstakes route". Following this concept Simons (1972), Napier (1970a), Hill (1957), and Stirton (1951) suggest that the early Neotropical primates crossed the marine barrier separating the two continents by being carried on rafts of floating forest vegetation such as mats of tree trunks which were dislodged from their original environment, perhaps by such natural forces as tropical storms.

The problem which is raised by these speculations is that no fossils in Central America have been found which could play an intermediate role to definitely link the nearctic omomyids to the neotropical primates. This could be related to either of two possibilities: (1) the intermediate fossils have not yet been discovered, or (2) the nearctic omomyids are not ancestral to the South American primates. Hoffstetter (1972) and Sarich (1970) tend to agree with the latter of the possibilities. Hoffstetter (1972) suggests that primitive monkeys with an African origin rafted across the Atlantic ocean to South America towards the end of the Eocene. He bases this supposition on the anatomical resemblances such as identical dental formulas and resemblances of the skeletal structure of the extinct neotropical monkeys with the extinct African monkeys. In relating to the problem of the considerable distance between Africa and South America, Hoffstetter emphasises that successful rafting depends more on marine currents rather than the actual distance being covered. He considers that the flow of the Atlantic-Pacific oceans (which were connected during the Eocene when the rafting most occurred) was in an east to west direction due to an equatorial current. Such a current would inhibit rafting from the north to the south (eliminating the possibility of a primate immigration from North to South America) and enhance a rafting from east to west, that is, a rafting from Africa to the coasts of Brazil.

Sarich (1970) bases his postulation of Ceboid origins in Africa on immunological evidence which endorses a divergence between the Old and the New World monkeys no later than 35 to 40 million years ago. The importance that these data seems to be that parallel development would not be able to explain the genetic continuity of the platyrrhines and catarrhines. (Parallel development would have to be the explanation of the similarities of the Old and New World monkeys if the ceboidea had evolved from the nearctic omomyids.) Only a common ancestor found in Africa would be able to explain this supposed genetic continuity.

In reality, the question of the ancestry of the Ceboidea will remain problematical until these hypotheses are proved or disproved. Those who discount an omomyid ancestry for the Ceboidea are, however, an exceptionally small minority. For the purpose of clarity, the majority opinion which will be accepted here is that the neotropical primates held a nearctic ancestry, from animals which reached the southern continent by rafting.

Paleontological Ancestry of the Tree Shrew

Uncertainty exists surrounding tupaiid phylogeny which is the result of an inadequate fossil record (Sorenson, 1970; Jenkins, 1974). There are several differing opinions of the ancestry of the tupaiids. Van Valen (1965) states that *Adapisoriculus* may be referred to Tupaiidae on the basis of dental and skull characteristics (21 out of 23 trends were convergent). *Adapisoriculus* is considered to be a late Paleocene specimen with fossil findings in middle Paleocene deposits in France, and early Eocene deposits in Belgium. Van Valen (1965) has found also that when *Adapisoriculus* and the Paleocene primates are compared on the basis of similar dental and skull characteristics, only 8 out of 20 trends were in agreement. He therefore concludes that the evolutionary trends leading to *Adapisoriculus* were not especially similar to those leading to Paleocene primates, while the recent tupaiids agree almost without exception with these trends. The comparison of the early primates with *Adapisoriculus* (which would not be materially changed if recent tupaiids were presented rather than *Adapisoriculus*) suggest the possibility that these similarities are all or nearly all the result of primitive retentions or independent acquisitions.

Szalay (1968), on the other hand, finds *Messelina* as one of the most likely fossil tupaiid candidates. In his opinion, *Adapisoriculus* may or may not be tupaiid. The lower teeth of *Messelina* are at least as similar to tupaiid lower dentition as are those of *Adapisoriculus*. Also, Szalay considers the upper teeth of *Messelina* to bear a much more striking resemblance to the unworn dentition of *Ptilocercus* (the most primitive living tupaiid) than do those of *Adapisoriculus* to the upper dentition of any recent species. It is Szalay's opinion that the dentition of *Ptilocercus* does not resemble the dentition of the primitive and early prosimians such as the plesiadapids. He states, therefore, that tupaiids are definitely not primates (Szalay, 1968, 1975). The insectivore-primate transition was probably created at the end of the Cretaceous or earlier by behavioral and physiologic adaptations. As behavioral modifications (partial preference for fruit, leaves, etc., as opposed to a predominant insectivorous diet) affected feeding habits and behavior, selection gradually operated to alter the morphology and function of feeding mechanisms.

Mc Kenna (1966) on the other hand, regards tupaiid as leptictid-like insectivores with special similarities to the Malagasy lemurs, Adapis and Northarctus, and are the closest relatives of the primates.

Until the uncertainty regarding the phylogeny of the tupaiids has been clarified, it will be impossible to discover the arboreal or non-arboreal ancestry of Tupaia glis.

Paleontological Ancestry of the Grey Squirrel

The first evidence of fossil rodents (a single lower molar tooth and some incisors) were found in wester North America in late Paleocene deposits (Wilson, 1951; Wood, 1950, 1959, 1962). This fossil is from the family Paramyidae which survived into the Eocene. The fossil remains of other fossil members of this family demonstrate that they were most likely to be small scampering animals. The paramyids, as a group, radiated to fill many niches throughout North America and Europe even though they were rather unspecialized. As to the question of whether or not these forms were terrestrial or arboreal, the skeletal remains show no specific structural adaptations to indicate either (Wood, 1962).

The structure of these fossils indicates that by the late Paleocene, the order of rodents had already evolved enough to fully differentiate itself from any of the other mammalian orders. There appears to be a question of what is the intermediate form lying between the paramyids and the basal mammalian stock. Wood (1962) suggests that the ancestral stock of the rodents lies close to the ancestral stock of the primates, the plesiadapids, due to the number of similarities shared between the plesiadapids and the paramyids. Simons (1963) and Van Valen (1965) agree with Wood's supposition of the closeness of the two lines of fossils. Kurten (1972) carries this supposition even further in suggesting that the true rodents may have evolved from the plesiadapids. Szalay (1972: 105), however, states that "there is no meaningful resemblances between the two families in details of the dentition, cranial morphology, or the basicranium". Thus a controversy exists as to the true origin of the rodents.

The genus <u>Uriscus</u> (family paramyidae) is a North American Eocene primate which appears to be the ancestral form of the sciurids. The molar pattern of this animal is so close to <u>Sciurus</u> that the two probably could not be generically separated if judgment was made on tooth structure alone (Wood, 1962, 1965). In general, the paramyids are more closely related to the sciurids than to any other family of rodents.

During the early Oligocene, the first true members of the squirrel family appear in the fossil record. The record of these animals are poorly known and few in number during this period. <u>Protosciurus</u> is known from Montana and Nebraska: its dentition reveals that it is close to the line of the tree squirrels. During the Miocene, more genera of sciurids, such as Miosciurius and Sciurus, are known in Europe and North America than during any other period of the squirrels' history (Black, 1972). According to Black (1972), these animals evolved in what was probably a broad-leafed evergreen to mixed deciduous forest environment and they were arboreal to semi-arboreal nut, seed, and berry feeders. After the Miocene, however, the history of the tree squirrel is essentially blank until the Pleistocene when modern forms appear. It was during this earlier period, however, that the squirrels migrated to Europe and Asia. It was not until the Pleistocene that the squirrels reached South America (Simpson, 1969).

Summary

The available evidence suggests that the early mammals were small, scurrying creatures which were principally terrestrial in habit. Primitive mammalian adaptations appear to have been something like that seen in extant tree shrews and the living insectivores.

By the time of the Paleocene, various placental lineages began to develop dental modifications suggestive of a diet which included great amounts of vegetation. Plesiadapis was evidently a herbivore which resembled the tree squirrel in habitat and locomotion. While much of the remaining paleontological ancestry of Saimiri is incomplete it is generally considered that the platyrrhine ancestors migrated southwards from North America as their tropical forestrial environment declined southwards. There is no fossil evidence related to Saimiri to indicate any adaptations to a terrestrial environment.

An inadequate fossil record of the tree shrew leads to uncertainty in determining tupaiid phylogeny. Until this uncertainty is cleared, it is impossible to discover the arboreal or non-arboreal ancestry of Tupaia glis.

Analysis of the fossil record of the squirrels suggest that the paramyids of the late Paleocene were the earliest rodent ancestors. There still remains, however, a question of whether these forms were terrestrial or arboreal. The next known sciurid fossil records are found in the Oligocene where, again, arboreality or terrestriality could not be determined. However, the fossil record indicates that Miocene ancestral forms were indeed arboreal.

Thus, while the continuation of arboreality cannot be accurately determined for these three genera, there is no indication that they were ever terrestrial after their evolution from the basal mammalian forms.

CHAPTER III

PALEO- AND RECENT ECOLOGICAL HABITATS OF THE SQUIRREL MONKEY, THE TREE SHREW, AND THE GREY SQUIRREL

General Paleo-ecological Conditions

The earth has been characterized by a constant fluctuation between warm and cool climates throughout its geological history. The period extending from the later Mesozoic to the Cenozoic era, that is, from the Cretaceous period to the Recent epoch (Table 1, Page 12) is especially important in studying the evolution of placental mammals since it was in this time zone that the various modern mammalian genera radiated from the ancestral mammalian stock. The various radiating mammals had to evolve to fit their various niches which were changing not only due to geological fluctuations, but also to the accompanying climatic fluctuations.

The period when the early mammals began to diverge from their early placental ancestors was one characterized by several earth movements. At the end of the Cretaceous, the Caramide Revolution raised the low-lying land and seas and produced the initial folding of the earth which would produce the mountain ranges now known as the Alps, the

Himalayas, and the Cordilleras (Napier, 1970a). Scientific discussion focuses on whether or not the formation of these mountain ranges were caused by collisions due to plate tectonics, the geological process which is believed to be responsible for continental drift.

It was at the end of the Cretaceous that the continents-as we now basically know them took their present latitudinal and longitudinal position on the earth through the continuing process of continental drift. The theory of continental drift holds that the outer shell of the earth, the lithosphere (which is some sixty miles thick), is segmented into six major plates each of which may encompass a continent and part of an adjacent ocean basin. The lithosphere behaves as if it were floating on a plastic layer, the asthenosphere. Continental drift occurs when a rift in the ocean floor allows molten rock to come up from the asthenosphere and forms a spreading ridge. The continents are then rafted apart at a rate up to twenty cm. per year (Mc Kenzie and Sclater, 1973; Rona, 1973). In following the possible validity of this theoretical geological process, it appears that all the continents were formed together as a single land mass, Pangaea. Gondwanaland, which included South America, Africa, India, Antarctica, and Australia was separated from the rest of Pangaea known as Laurasia. Two extensive rifts which were formed no longer than 200 million years ago resulted in the openings between the southern hemispheral land mass which created the Atlantic and Indian Oceans. South America and Africa together split away from Antarctica, Australia, and India approximately 180 million years ago. At the close of the Jurassic, a rift splitting South America from Africa began in the south and ended eventually in the north as far as Nigeria (Dietz and Holden, 1970; Martin, 1969; and Darlington, 1965).

Undoubtedly, these geological changes played a great role in determining the climatic fluctuations during those time periods. Throughout most of the history of the earth, the temperature had been much warmer than what is known today (Schwarzbach, 1961; Butzer, 1971). During the Cretaceous across the earth, the temperature was uniformly high and humid throughout the year. Tropical and subtropical conditions extended far to the north to 53° north latitude (Napier, 1970a). Evidence yielding fossil remains of spruce, hazel, and poplar trees found only 8° from the North Pole suggest that throughout the Arctic at this period, the temperature was characterized by a cool-temperate climate (Cracraft, 1973; Napier, 1970a).

It is, however, at the Cretaceous-Paleocene boundary where a cooling trend is noted. This trend is characterized by a net southerly migration of the subtropical flora of about 5° of latitude (Cracraft, 1973). Seasonality in the high and middle latitudes became more predominant. Where previously there had occurred a uniformity of temperature throughout the year, there became a distinct difference between cold winters and warm summers.

By the beginning of the Eocene in North America, the territory as far north as Oregon was still subtropical. The area was characterized by subtropical evergreens and numerous subtropical oaks (Butzer, 1971). These forests were intermediate in type between a modern tropical rain forest and a warm temperate flora similar to that of the tropical rain forests of Panama and the temperate rain forests of Costa Rica (Andrews, 1961). Coral growth was possible in the oceans at the same latitude. To the south of this throughout the territory surrounding what is now Wyoming and Utah, the climate was cool, with moist winters and relatively long, warm summers. The termperature fluctuated widely with a resulting annual mean temperature of 65° F (18.3° C). The flora was predominated with subtropical types especially with many forms like palms which would have required much rain and warmth (Gazin, 1958). North of this 50° latitude up to 70° was a land dominated by a coniferous-type of forest composed predominantly of the Sequoia species with also pine, fir, spruce, willow, birch, and elm. This area was characterized by a mean annual temperature of 10° C (50° F) with a July mean of 18-21° C (64.4 - 69.8° F) (Butzer, 1971).

Little is known of the climatic changes during the Oligocene, but the evidence does indicate that the cooling process across the earth began to rapidly accelerate. The tropical or subtropical forest in Oregon in the Eocene no longer occurred north of southern California. The former subtropical floras were being replaced by a temperate flora of oaks, beeches, and giant conifers (Napier, 1970a). The subtropical forests then reached no further than Central America (Napier, 1970b).

During the middle of the Miocene, there occurred a short-lived warming period followed by a further cooling process. By the upper Miocene, the average temperature of the world was approximately the same then as it is presently except for the fact that the summer maxima was reduced and the winter minima increased so as to leave a small fluctuation between the seasons. During the Miocene the Artic zone increased at the expense of the tropical areas. The increasing polar ice cap produced a cold trend in the Late Miocene which intensified throughout the Pliocene, culminating in the Pleistocene glaciations (Napier, 1970a).

The effect of these climatic changes on the distribution of areas which could support a tropical rain forest was dramatic. In the Eocene, subtropical and tropical forests spread 50° latitude north and south of the equator producing a total tropical belt of 100°. However, the area today which could support these kinds of forests has shrunk to less than 50°, and many areas in this region are either deserts, grasslands, mountainous regions, or high plateaus.

The actual area of tropical forest found today is computed to be less than five percent of what it was in the Paleocene (Napier, 1970b).

An important factor which accompanied the climatic change was the change in the kind of vegetation that inhabitated the forests. During the Cretaceous, angiosperms gradually replaced the gymnosperms as the predominant plant form (Axelrod, 1952). By the time of the Paleocene epoch, the angiosperm trees which were almost identical to modern species dominated the vegetation, with the evolution of such genera as the maples, sycamores, oaks, figs, birches, and magnolias (Eyre, 1963). The important point here is the botanical differences between the gymnosperms and angiosperms. Angiosperms produce both flowers and fruit (which include what is known as nuts, fruits, gains, and vegetables) while gymnosperms do not (Hill, Popp, and Grove, 1967).

Summary

The spread of the flowering plants during the Cretaceous opened new niches to insects. The insect faunas of the forest canopies (where the nector, pollen, and fruit are primarily available) came to rival those of the forest floor. Both insects and fruit in the canopy layers were soon exploited by the Cretaceous mammals. Adaptations to these conditions set many of the basal patterns which were to be refined in the various mammalian evolutionary history.

General Recent Ecological Habitats

Since the squirrel monkey, the tree shrew, and the grey squirrel are arboreal animals, their habitats are located in forests; however, these are forests of different ecological types. The squirrel monkey is situated in a South American rain forest (which is similar to the Indonesian-Malayan forests in which the tree shrew is located) while the grey squirrel is generally found in the temperate deciduous forest in the eastern section of the United States.

The Tropical Rain Forest

Presently, tropical rain forests occur in three main areas on the earth: (1) the Amazon and Orincoco basins in South America and the Central American isthmus, (2) the Congo, Niger, and Zambezi basins of central and western Africa and Madagascar, and (3) the Indo-Malay-Borneo-New Guinea regions. These rain forests differ from each other in the kinds and numbers of species present, but the forest structure and ecology are similar in all three areas (Richard, 1973; Odum, 1971). Therefore, a discussion about the general structure of any of these forests will relate to the structures of all the forests.

According to Odum (1971), tropical rain forests are characterized by having an excess of 80 or 90 inches of rainfall distributed throughout the year, interspersed with one or more relatively dry seasons. They are also characterized by the constancy of their temperature whereas the variation in temperature between winter and summer (an annual mean in summer may be 81°F while in winter it is 80°F (Haddow, 1952) is less than the variation in temperature between night and day. For this reason, both young and old leaves may occur on the same tree throughout the year. The buds producing these leaves are not subject to the cold and drying winds as are the buds in the north. Jungle trees, therefore, produce fewer but larger and more succulent buds than trees in the temperate zone (Richards, 1970).

Rain forests are known to have many of the largest trees of any forest as they normally average a height of more than 150 feet, a noted exception being the Sequoia species located in the Sierra Nevadas on the western coast of the United States. The entire canopy layer of this forest may be divided into three different horizontal strata. The heights of which are relative as soil and water conditions can greatly affect them. These storeys can generally be described as: (1) the under storey which ranges in heights from 25 to 50 feet, (2) the middle storey which ranges in heights from 50 to 120 feet and (3) the upper storey which ranges in heights from 120 to 150+ feet (Richards, 1970, 1973; Napier & Napier, 1967).

The presence of trees ranging in various heights is especially important in providing different environmental conditions for animals which inhabit various strata of the forest. The upper storey contains trees with broad umbrella-like crowns, that is, they are wider than deep. The upper storey forms a discontinuous or open strata of the canopy. The importance of this layer for animals is that the maximum density of fruits and leaves tends to be found on the periphery of the limbs far away from the trunk. The under storey contains trees whose crowns form a completely closed canopy, that is, the crowns are in contact with or overlap with one another to form a continuous stratum. The crowns are deeper than they are wide with the fruit and leaves distributed throughout the trees rather than peripherally as in the upper storey. The middle storey consists of an irregular layer of trees whose crowns are just in contact with one another as in the under storey and contains the same distribution of fruit and leaves (Napier & Napier, 1967). The main difference between the middle and under storeys is the heights of the trees.

Important to the middle and under storey is that the individual trees are usually connected to one another by great woody plants (lianas) that are rooted in the soil but depend on trees for support. Lianas commonly reach a length of over 200 feet. Their dependence on the tropical trees is, however, not parasitic but rather, symbiotic. The roots of tropical trees are generally shallow with most of them being located within the top three or four feet of soil. The greatest concentration of fine roots (which are the most active in the absorption of nutrients) are found in or just below the thin layer of constantly decomposing materials at the soil surface. The reason for this shallowness is due to the leaching of nutrients from the soil because of the heavy tropical rains. There are, therefore, no enormous root systems to firmly anchor the trees to the ground. The importance of lianas is that they support the trees by linking one tree to another to form a vast interlacing network. These networks are so supportive, in fact, that they are able to hold a tree up even after its base has been cut (Richards, 1970, 1973).

Temperate Deciduous Forest

Characteristic of the temperate deciduous forest is a much lower annual rainfall than the rain forest. The per annum rainfall ranges from 23 to 40 inches distributed evenly throughout the year (Cleland, 1966). The temperature varies greatly throughout the year and may range annually from means of 7°F in the winter months to over 68°F in the summer months (Haddow, 1952). Due to this radical change, the broad leaves on the trees are lost in the fall with the next season's leaves growing from buds that are fully formed by the end of summer. These winter buds are in a kind of hard protective seal to protect them from the cold during the winter (Richards, 1970).

The trees of the temperate forest generally range from 75 to 100 feet (with the noted exception being the

Sierra Sequoias). There exists in the forest only two horizontal strata among the canopy; the higher canopy layer contains the mature trees while the lower canopy layer contains young or suppressed trees of large species and the normally small species (Shelford, 1963). It is characteristic of both these storeys to contain trees which produce a lot of pulpy fruits and nuts (Odum, 1971).

There is no need for the symbiotic relationship of the supporting networks of lianas since the root system of each individual tree itself is great enough to firmly anchor the tree to the ground. For example, in a small apple tree, its root system reaches both vertically and horizontally through the soil to a depth of twelve feet (Epstein, 1973).

Summary

Floristically, the tropical rain forest is extremely varied. Growth is luxuriant throughout the year. Competition for sunlight thus becomes intense. A premium is placed on rapid growth up to the forest canopy, where sunlight becomes available. There is, therefore, little side branching until the canopy is attained, whereupon the tree opens out into a crown of leaf-bearing branches. Trees of the under storey forms normally bear their fruits and seeds at the tips of thin shoots of current growth. Lianas connections between the trees are abundant in the tropical rain forest.

The temperate deciduous forest is not as varied floristically as the rain forest. No leaves, fruits or buds are produced at least part of the year due to climatic factors. There are only two storeys identified in this type of forest (an upper and a lower storey). Both these storeys bear many pulpy fruits and nuts. Lianas connecting the trees are not present in this type of forest.

CHAPTER IV

PHYSICAL AND BEHAVIORAL DESCRIPTION OF THE EXPERIMENTAL ANIMALS

The Squirrel Monkey (Saimiri sciurius)

The order of primates is divided into two suborders: the Prosimii and the Anthropoidea. The suborder Anthropoidea is further divided into three superfamilies: the Hominoidea and the Cercopithecoidea (these two can be referred to also by the infraordinal term Catarrhini or the Old World primates) and the Ceboidea (which can be referred to also by the infraordinal term Platyrrhini or the New World primates). Extant species of platyrrhini are restricted to the New World, specifically Central and South America. These species appear to be extremely sensitive to temperatures below 70°F (Napier & Napier, 1967). The squirrel monkey, Saimiri sciurius (subfamily Cebinae family Cebidae), is the platyrrhine that is the subject animal in this thesis.

Distribution

Squirrel monkeys are found between the 10° north latitude and 15° south latitude, namely Costa Rica, Panama, Paraguay, Columbia, Eduador, Peru, Bolivia, Venezuela, Guyana, Surinam, French Guiana, and Brazil (Cooper, 1968).

Physical Characteristics

The squirrel monkey is among the smallest of the Cebidae. Its ventral fur is short and dense and has a coloring that is usually of various shades of grey-green or olive. The dorsal side of its body and limbs are white, yellow or orange and the end of the tail is black. The face is usually white with a dark muzzle. The tail is thick at its base and frequently tufted at the tip (Hill, 1960; Napier & Napier, 1967).

Saimiri sciurius weighs from 365-750 gm. The male's head and body length ranges 249-370 mm with the female being slightly smaller. The squirrel monkey's tail adds another 367-465 mm to the total body length.

Rose (1974) classifies the squirrel monkey's tail as a hair-covered prehensile one; i.e., the tail is used in a prehensile way by adult monkeys during postural activities and by infants who wrap their tail around their mothers' bodies or tail bases while being carried in a ventral position. This is, however, an unusual way of describing prehensility. In general, the squirrel monkey's tail is described as non-prehensile (Hill, 1960). The squirrel monkey is very dolichocephalic when compared to other cebids (Hill, 1960). Squirrel monkeys have a large skull, and of all mammals, they have the greatest brain weight per body weight ratio with their brain composing 12.5 percent of their body weight (a ratio of 1 to 8) (Tobias, 1971). Their face is orthognathous, and their ears are often tufted. Their legs are markedly longer than their arms (Napier and Napier, 1967).

Social Grouping

The reported size of a squirrel monkey troop varies to a considerable extent. Thorington (1968) reports troops ranging from eighteen to twenty-two monkeys, Jolly (1972) reports troops ranging from fifty to one hundred animals, and Hill (1960) reports troops may be found to reach limits of up to five hundred. This wide range of reported size is probably due to local environmental conditions plus other variable factors. It is agreed, however, that large troops, assembled for the night to sleep together, would separate into much smaller groups during the day when foraging and feeding (Thorington, 1968; Du Mond, 1968; and Mason, 1971).

Activity Patterns

Although they are considered to be arboreal, squirrel monkeys spend a large amount of their time on the ground foraging and engaging in play activities; however, in any kind of danger or stressful situation, they move rapidly into the trees. The monkeys are not found on open ground more than a few feet from the trees. It appears that they find many insects on the ground, and during mating season they spend more than half the day on the ground with the adults foraging and interacting socially while the juveniles play. Play initiated in the trees usually occurs at levels no higher than ten feet. Often, once play is initiated, the animals descend to the ground. The monkeys never sleep or rest on the ground (Du Mond, 1968).

Squirrel monkeys are diurnal with an activity peak in early to midmorning and again during middle to late afternoon. In the middle of the day they are less active and generally rest for one to two hours. In early morning they range to the tops of the trees and sometimes are active at the very top of the canopy. Later in the day they move below the canopy (Thorington, 1968).

Food Resources

The monkeys' main food items are flowers, fruits, nuts and berries. Frequently they eat fruit where it is located, but at times they carry it in one of their hands to another place to eat it (Thorington, 1968). They also eat a wide variety of insects including flies, butterflies, mosquitoes, spiders, and beetles (Hill, 1960; Thorington, 1968; and Du Mond, 1968). Squirrel monkeys also have been noted to eat snails, land and tree crabs, tree frogs and small birds (Hill, 1960). They do not ordinarily drink from streams or bodies of water but learn to recognize certain trees with water holes which have been formed by rotting areas where branches have broken off. They insert their hand or forearm, withdraw it, and lick the water off their fur or out of their hand. They also lick rain and dew directly from leaves (Du Mond, 1968).

Locomotor Activities

In terms of general locomotion, the squirrel monkey is a quadruped. Quadrupedalism is important to the theory of arboreal specialization. According to Napier and Napier, quadrupedalism is:

> . . . a type of locomotion which can take place on the ground or in the trees. Its principle component is four legged walking or running. In an arboreal situation, the hands and feet may be used in a prehensile fashion, to provide stability. The movements of springing, jumping, and leaping are associated with this mode of locomotion. Quadrupedalism also involves the vertical movement of climbing while using all four extremeties. Movement may be rapid or it may be cautious and slow. Quadrupedal primates in certain situations show a variable amount of arm swinging with or without the use of a prehensile tail . . . (There are five subtypes of quadrupedalism) . . . (1) Old World semibrachiation, (2) New World semibrachiation, (3) ground running and walking, (4) branch running and walking, and (5) slow climbing. . . Branch running and walking is defined as a generalized quadrupedal locomotion in which running or walking in trees usually involves a prehensile grasp with the forelimbs or hindlimbs or both. The hand is usually plantigrade. Climbing, jumping or leaping in a dog-like fashion is also seen (Napier & Napier, 1967: 19).

Thus, while the squirrel monkey is defined as an arboreal quadruped, it is known to perform other locomotor activities such as quadrupedal ground running and walking, leaping and springing, vertical climbing, and at special occasions, a form of bipedal walking. However, these other forms of locomotion in the monkey's behavioral repertoire are not its usual or most frequent form of locomotion. Thus, the squirrel monkey is characterized as a branch running and walking quadruped.

When the squirrel monkey is about to make a very long leap such as from branch to branch or tree to tree, it flexes its knees, hangs its arms down and brings them slightly to the rear, and propels itself forward with the hindlimbs. It is not unusual for it to make a pinpoint landing on a smooth branch one fourth inch in diameter from a height of thirty feet. The monkey, in landing, can turn its body in flight so as to land in perfect alignment with the branch, using the springiness of the branch to break the impact of landing (Du Mond, 1968).

As stated previously, the hindlimb of the animal is used as a thrusting mechanism to give the animal momentum as it leaps. The forelimb is used more as a pulling, suspending, and manipulating appendage with the added ability of a wide amount of lateral movements. The forelimbs permit a wider range of motion than the hindlimbs because they are connected with the freely movable shoulder girdle instead of the more stable pelvic girdle (Schultz, 1969).

Postural Positions

Squirrel monkeys have, in their behavioral repertoire, various postures used in connection with different activities during the day. The posture used when the animal rests during the day or sleeps at night is called the "huddle". While in this position, the animal crouches on its hind legs, hunches its back and supports the upper torso with flexed arms as the animal leans forward. The tail is brought around underneath so the animal is sitting on the base of it with its end curled around to the front. It is then placed over one of the animal's shoulders. A second position used in the trees is a sprawling posture. This is used when the animal straddles a branch, resting on its vertical surface, and letting its limbs and tail dangle below. (A similar position is known for the squirrel.) This position is never used for sleep, but only when the animal is resting and sunning itself. Squirrel monkeys do not ordinarily walk or stand bipedally, but they occasionally do so if they are carrying something large enough to require the use of both hands. When handling an object, the monkey assumes a semi-huddled position, squatting on its haunches, freeing its hands for manipulating and carrying the object (Du Mond, 1968).

Structure of the Manus

The manus of the squirrel monkey retains a primitive pentadactyl condition (Midlo, 1934). All five of the digits are terminated on their dorsal side with flattened nails or ungulas. Le Gros Clark (1936, 1959) states that the flattened nail is a degenerative form, a retrogression from the structure of the claw. In the squirrel monkey the nails are narrow and compressed (Pocock, 1920) making them appear to approximate a fully developed claw (Le Gros Clark, 1936) (Plate 1).

The squirrel monkey does not have vibrissae to aid in tactile perception nor does it have separate and distinctive volar pads in the palms of its manus. There are no hairs nor sebaceous glands found on the palms. The volar pads in primates are quite indistinct (Hepburn, 1892) and they have a special differentiation of the epidermis and the dermis with papillary ridges, many sweat glands with the openings ending in rows on the papillary ridges, a network of nerves, and a vast complex of sensory nerve endings (Midlo, 1934; Winkelman, 1962; and Biegert, 1971) (Plate 2).

The papillary ridges, according to Cauna (1954), are covered by a soft layer of cells called that stratum corneum. This layer swells in aqueous solutions including sweat. In the grooves, however, between the ridges the stratum corneum is hard. It provides a supporting framework for the tactile ridges. Pressure receptors primarily concerned with tactile discrimination, called Meissner's corpuscles, are located in the dermal papillae. The epidermis is raised into elevations superficially to the corpuscles. These are the first

Plate 1. Dorsal view of the manus of _Saimiri sciurius_. (Measured in centimeters.)

Plate 2. Ventral view of the
manus of <u>Saimiri sciurius</u>.
(Measured in centimeters.)

contact points for the papillary ridges (Cauna, 1954). The combination of all these structures supplies the manus with an elastic cushion with ridges and a moistened surface which provides the animal with special frictional capabilities which are necessary when climbing, and also supplies the animal with special tactile abilities (Biegert, 1963, 1971).

The tactile sensations supplied by the friction skin of the manus are much more delicate, varied and informative than are the tactile sensations supplied by the vibrissae of the squirrel and the tree shrew (Pocock, 1914; Schultz, 1969). Le Gros Clark (1959) states that the more primitive tactile organs (the vibrissae) have been gradually replaced by the development of the tactile pads. "These pads were acquired as a secondary result of the transformation of sharp claws into flattened nails, a transformation which was primarily related to the need for a more efficient pliability in the grasping functions..." (Le Gros Clark, 1959: 214). Flattened nails provide a much more efficient grasping mechanism for the animals and can be adapted with much more precision to surfaces of varying shapes, sizes and textures.

Napier and Napier (1967) classify the manus of the squirrel monkey as convergent and prehensile with a pseudo-opposable thumb. They define convergence as:

> . . . a compound movement occurring at the metacarpo-phalangeal joints and consists of the flexion and adduction leading to the approximation of the tips of

> the digits; the opposite movement is divergence, a movement of extension and abduction to leading of a fanning of the digits (Napier & Napier, 1967: 196).

Prehensile hands are convergent hands that come together in such a manner that an object may be grasped and held securely by one hand. There are three main types of prehensile hands: (1) those with non-opposable thumbs, (2) those with pseudo-opposable thumbs, and (3) those with opposable thumbs. If only function and behavior were considered in analyzing the second and third types of prehensility, then both would be regarded as opposite in the sense that the thumb can be directed towards one or more of the remaining digits so that the palmar surfaces of the thumb and the fingers lie parallel and opposite each other. However, when the second and third type of prehensility are analyzed in regard to morphology, the difference between the two is considerable. The main difference is that in the pseudo-opposable thumb, rotation at the carpo-metacarpal joint is lacking. It appears that the articulation at this joint in the pseudo-opposable thumb is a "hinge" type joint in contrast to the "saddle" joint found in the truly opposable thumbs of the catarrhines (Napier, 1960; Napier & Napier, 1967).

The Tree Shrew (Tupaia glis)

The taxonomic placement of the tupaiids has been under discussion for the past several years. Van Valen (1965) uses paleontologic evidence (which is described in detail in the paleontological history of the tree shrew) to dispute primate-tupaiid relations. Another scholar disputing primate-tupaiid relationships is Hill (1965) who bases his opinion on the embryologic differences of tupaiids and primates. Martin (1966, 1968) militates against a primate affiliation of the tree shrew due to the maternal behavior of the tupaiids. The female tupaiid gives birth in a nest separate from the parents' sleeping nest, abandons the young for one or two days, returns at 48-hour intervals to squat over the young, squirt milk into their mouths for approximately ten minutes, and then is off again. On these grounds, Martin concludes that the tree shrew is not closely related to the primates and is best classified as being in a separate order of mammals (Tupaioidea) who show significant similarities to Marsupialia. Campbell (1966) argues on the basis of neuroanatomy of recent tupaiids the convergent evolution with the primates. Szalay (1972) concludes by the combined criteria of teeth and ear regions of the skull that the Tupaiidae should not be viewed as primates.

On the other hand, Le Gros Clark (1959) classifies the tree shrews as one of the superfamilies (Tupaioidea) of the Lemuriformes, and reasons the tree shrews show a much closer approximation to typical lower primates than do any of the Insectivora. Buettner-Janusch (1966) states that the tree shrew represents the kind of mammal that very probably was the kind which the primates developed. Goodman (1963) concludes that immunological studies of serum proteins indicate closer affinities with primates than with any other mammalian group.

Thus, as noted above, the taxonomical placement of the tree shrew is under heated controversy and it is beyond the scope of the present study to determine the validity of any of the above theories.

Distribution

The particular tree shrew discussed in this paper, *Tupaia glis*, can be found in southeast Asia, specifically in India, north of the River Ganges and south of the Himalayas, Burma, southern and western China, Indo-China, Thailand and Malaya; also, on the islands of Harran, Sumatra, Java, Borneo, Bali, and the Philippines (Napier & Napier, 1967; Hill, 1972; Jenkins, 1974).

Physical Characteristics

Tree shrews have a superficial resemblance to squirrels. The generic term is derived from the Malai word *tupai* which means a squirrel (Le Gros Clark, 1959). However, the tree shrew is readily distinguished from the squirrel by the absence of long, black whiskers and by having a longer nose (Walker, 1964). *Tupaia glis* has a small body and short arms and legs. The male averages about 177 gm in weight with the head and body length ranging from 140 to 230 mm. The tail is bushy and is approximately equal to the head and body length; thus, the tail may add an additional 129 to 215 mm to the total body length (Napier & Napier, 1967).

The dorsal fur of the tree shrew is ocherous, reddish, olive and shades of brown and greys to almost black. The ventral fur is whitish or buff. It often has an oblique pale shoulder stripe (Walker, 1964).

The tree shrew has a slender build, comparatively short limbs (especially the anterior pair), small hands and long feet (Schultz, 1969). The tail is long and bushy and is used as a balancer in arboreal activities (Zuckerman, 1932; Le Gros Clark, 1959; Hill, 1972). Tupaia glis has short whiskers and an elongated shrew-like nose which terminates in a naked moist snout which acts as a tactile organ (Zuckerman, 1932).

Social Grouping

Observations of Tupaia glis have shown that it does not form large social groups; rather, it forms only short-lived family units (Cantor, 1846; Sorenson, 1970); and even these family units are broken up by paternal aggression towards the young (Sorenson, 1974). Natural populations of Tupaia glis in Thailand reach only 15 to 30 individuals per acre (Morris, 1967). Sorenson (1970) believes that the small size of the social unit of the tree shrew is related to the limited conditions of food supply occasioned by the stable conditions of the rain forest.

The adult tree shrew, especially the male is not a gregarious animal. The male and female maintain linear status hierarchies based on aggressive and agonistic displays. (However, this is found more among the males than the females.) These displays determine a single dominant animal who then assumes the role of despot. The ranking of this male is rarely reversed. The presence alone of this male has been found to disrupt all sexual behavior among the remaining animals. Following the establishment of this hierarchy, the overall aggression among the animals is decreased and rank is maintained by ritualized fighting patterns (Vandenbergh, 1963; Buettner-Janusch, 1966; Lim, 1969; Sorenson, 1970, 1974; Eisenberg, 1975; Moynihan, 1976). In captivity, it has been impossible to keep two or more male Tupaia glis in the same cage (Sorenson, 1974).

Activity Patterns

The tree shrew is an arboreal animal, however, it often feeds and rests on the ground and shrub level (Napier & Napier, 1967; Jenkins, 1974; Eisenberg, 1975). Its nests, for sleeping and reproduction, are found most often in tree holes and in crevices in rocks, (Napier & Napier, 1967; Lim, 1969; Kelso, 1974).

Tree shrews are diurnal (Schultz, 1969; Sorenson, 1970; Doyle, 1974; Charles-Dominique, 1975; Eisenberg, 1975; Moynihan, 1976). During the day, they alternate activity with rest periods. Tree shrews awake about 6:20 A.M. after which they eat, explore, and are active until naptime at approximately 11:30 A.M. Their major activity period occurs between 5 and 6 P.M. Temperature and humidity affect their activity levels; i.e., there occurs a decrease in activity with an increase in temperature (greater than 85° F) and humidity (Vandenbergh, 1963; Lim, 1969; Sorenson, 1970; Doyle, 1974).

Food Resources

Feeding patterns of the tree shrew have shown it to be an omnivorous animal (Le Gros Clark, 1959). It begins to feed in the early morning and continues to eat intermittently throughout the day (Sorenson, 1970). Their main food items are insects (such as cicadas and grasshoppers), earthworms, fruits (such as bananas, papayas, and young coconuts), seeds, and leaves (Hendrickson, 1954; Le Gros Clark, 1959; Walker, 1964; Morris, 1967; Napier & Napier, 1967; Sorenson, 1970; Hill, 1972; Chiarelli, 1973). Insects are trapped beneath the forefeet and eaten while held in this position or raised by both forefeet to the mouth (Sorenson, 1970). The tree shrew has also been observed to show great skill in attacking and killing mice and to consume almost the entire animal (Le Gros Clark, 1959). Adult tree shrews have been found to be cannibalistic and eat both newborn animals and other adults which have died (Sorenson, 1970).

evidence of food hoarding (Sorenson, 1970).

The intake of water is directly related to the increase of temperature and/or activity; i.e., water consumption increases with an increase of temperature and after periods of hyperactivity (Sorenson, 1970).

Locomotor Activities

Little data of the tree shrew locomotor activities have been gathered, possibly because of its small size and shyness; but, also because of its apparent tendency to territorial restrictions (Jenkins, 1974). Tupaia glis is, however, considered to be a generalized arboreal quadruped (Stern, 1973). It is characteristic of the tree shrew to be very quick and agile in its movements and to have the ability to run, climb, and leap with astounding dexterity (Schultz, 1969). It employs rapid, jerky, scurrying movements on the ground or in trees, rather like a rodent (Vandenbergh, 1963; Napier & Napier, 1967). Jenkins (1974) reports of considerable agility in the arboreal-terristrial patterns of the tree shrew. It can run over the ground in long straight dashes, doubling sharply to avoid pursuit. It can climb with great agility and balance and leap on fine supports. Upward leaps of 1.2 m have been observed (Vandenberg 1963; Sorenson, 1970; Doyle, 1974). Tupaia glis is particularly adept at rapid locomotion in an environment which necessitates abrupt changes in direction or elevation (Jenkins, 1974).

The typical locomotor pattern used by the tree shrew is the primitive rebounding jump; i.e., the hindlimb weight is appreciably greater than that of the forelimb. The hindlimbs provide most of the propulsive thrust with the forelimbs acting principally as shock absorbers (Jenkins, 1974).

Postural Positions

Various postures typical of the tree shrew's behavioral repertoire have been observed. During exposure to high temperatures (85° F or higher), the tree shrew tends to sprawl in a position similar to the squirrel monkey and grey squirrel, with its body flattened dorsoventrally and its limbs fully extended. This is thought to aid in evaporative cooling. In contrast, during cooler months, the tree shrew can be found resting in a sunny spot along logs on the ground (Sorenson, 1970).

The tree shrew can be observed in three basic resting postures: (1) it positions itself high on an oblique tree limb, clasping the branch with its forefeet with its tail extending out behind it or forming an "S" curved along the branch; (2) it sits flat on surfaces with its tail curled around its body and its head resting on its tail; and (3) it sits on flat surfaces with its tail curled up and over its back with its head between its forelimbs (Doyle, 1974).

Another posture which the tree shrew assumes is that it sits upright when eating with its rear feet pointing out laterally and its tail extended directly backwards. Its shoulder slumps forward slightly and its forefeet are held with the palms facing up. It then holds food with its claws and the palms of its forefeet (Sorenson, 1970).

The tree shrew explores nearby objects in a horizontal, elongated posture in which the body and the tail are stretched tautly in a straight line with its nose thrust forward and its legs stretched out behind (Doyle, 1974).

As for a sleeping position, if the temperature is less than 85° F, Tupaia glis sleeps at night in a tightly curled ball. Several tree shrews (usually females) lie on top of one another in groups of two to five, sometimes puffing up their fur and assuming embryonic positions. If the temperature is greater than 85° F, the tree shrews rest separately, with their bodies flattened dorsoventrally (Sorenson, 1970; Doyle, 1974).

Structure of the Manus

The manus of the tree shrew retains the primitive pentadactyl condition. All digits are furnished with claws. The manus is typical of a generalized mammal being non-prehensile and capable only of convergence and divergence of the digits. Comparatively speaking, the tree shrew has short digits and long thumbs with the middle digit being the longest. The thumb should more appropriately, perhaps, be called the pre-axial digit which is hardly differentiated from the remaining digits either structurally or functionally.

The hand is not prehensile and the "thumb" is divergent but non-opposable (Napier & Napier, 1967).

The manus of the tree shrew is furnished with friction pads on its palmar surface, corresponding in number, arrangement and distinctness to the generalized mammalian condition. Proximally, there are two pads (thenar and hypothenar) and distally, four interdigital pads (Plate 3). All of these pads are covered by a fine pattern of papillary ridges and the skin is richly supplied with sweat glands. On the ulnar side of the forearm, immediately above the wrist, is a small skin papilla in which are situated the carpal vibrissae (Le Gros Clark, 1959). All hairs are to some extent tactile organs inasmuch as contact of the hair shaft with an external object automatically distorts the follicle, within the wall of which are nerve terminals sensitive to minute changes in pressure. Vibrissae are lengthened and strengthened hairs and their follicles are modified by the development around them of large venous sinuses. Contact of a vibrissa with an external object involves greater distortion of the follicle and this sets up pressure waves in the blood sinus which modify the effects of the surrounding nerve terminals (Hill, 1972).

The Grey Squirrel (Sciurus carolinensis)

The taxonomic order of Rodentia comprises a large number of subspecies numbering approximately 3,400. In fact, rodents

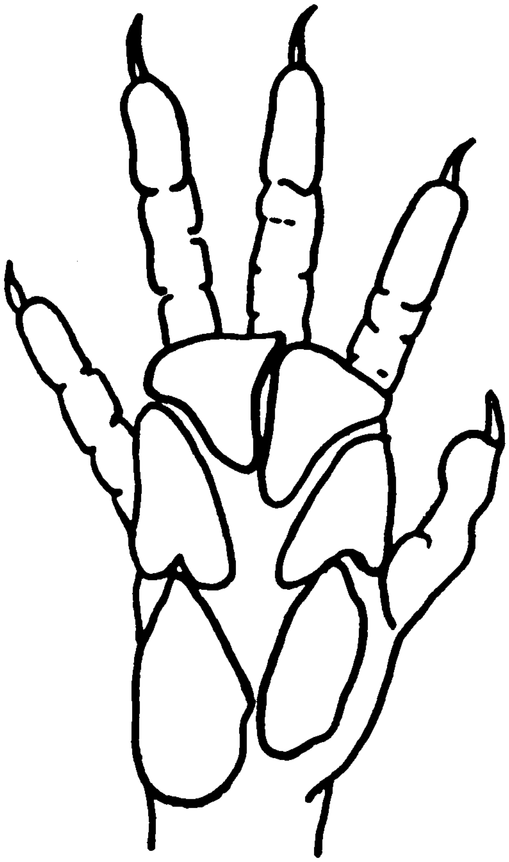

Plate 3. Ventral view of the
manus of Tupaia glis.
(Modified after Bishop 1964)
(Four times life size.)

include more than half of all kinds of living mammals (Shorten, 1954). Three suborders are included in this order: (1) the suborder Sciuromorpha which includes squirrels, gophers, and woodchucks; (2) the suborder Caviamorpha which includes the chinchilla, the Guinea pig, and some South American rodents and New World porcupines; and (3) the suborder Myomorpha which includes mice, rats, lemmings and hamsters (Romer, 1970). Within the suborder Sciuromorpha, five superfamilies are found: (1) Aplodontoidea, (2) Scuiroidea, (3) Geomyoidea, (4) Castoroidea, and (5) Anomaluroidea. The superfamily Scuiroidea in turn consists of a single family, Sciuridea (Simpson, 1945). Sciuridea is one of the largest families of living rodents, and has an almost world-wide distribution as it is found on every continent on the earth except Australia (Black, 1972). There are twelve genera of flying squirrels and thirty genera of tree- and ground squirrels (Shorten, 1954). The squirrel to be examined in the present study is the grey squirrel, Sciurus carolinensis.

Distribution

The grey squirrel is distributed throughout the entire United States east of the Mississippi. The grey squirrel is also located in Britain having been introduced as an alien species in the early nineteenth century (Shorten, 1954).

It appears that the distribution of grey squirrels in the United States is closely related to the distribution of eastern hardwood trees, especially the oak, hickory and chestnut (Hall & Kelson, 1959).

Physical Characteristics

The usually more visible dorsal parts of the animal are greyish mixed with a yellowish-brown color. Specifically, the head and the back of the animal is darker and possesses more of a brownish tinge than does the side of its limbs, back and rump which are for the most part greyish. The squirrel's ears are yellowish-white and are found most often without tufts at their tips. The hairs of the tail are yellowish at the base banded with black, tipped with white. The ventral parts of the animal are whitish in color (Anthony, 1928).

Sciurus carolinensis weighs from 400 to 700 gm. The male is usually about 462.5 mm in length with the female being slightly longer. The head and body make up from 250 to 375 mm of the total body length with the tail comprising the remaining length. The tail is never longer than the head and body (Shorten, 1954).

Social Grouping

Observations show that squirrels do not form long-lasting social groups even as small a social group as a family. When breeding occurs in the early months of the year, arboreal nests are occupied by pairs or groups of animals. However, once the female is impregnated, the male is no longer tolerated in the nest. Individual nests which have been inspected after the mating period, have been found to be occupied by as many as nine squirrels. The occupants of these nests usually are either mated males which were driven from their own nests by their females, or a group of young remaining in the nest in which they were born (Shorten, 1954).

Activity Patterns

The grey squirrel is a member of the group called tree squirrels. Tree squirrels are "those that nest above the ground in trees, take refuge primarily in trees when fleeing enemies, and obtain a substantial portion of their food from the fruits, buds, and other material of trees" (Moore, 1959: 154). These animals never rest on the ground for a prolonged period. The conventional home for the grey squirrel is a den within a hollow area of a tree (Shorten, 1954). If there is no such area, a nest of twigs and leaves is made where a branch forks from the trunk or in the smaller branches of the crown (Fitzwater & Frank, 1944).

Grey squirrels usually occupy a relatively small home range varying from 0.2 to 7.2 acres. The ranging activities of some squirrels, however, have been observed to cover as much as a five mile area (MacClintock, 1970).

Squirrels are diurnal animals. They have three peak periods of activity: (1) in the early morning, (2) midday, and (3) approximately an hour before dusk. It is during these periods that their locomotor patterns may be observed.

Food Resources

In addition to providing a protective home for the grey squirrel, trees also provide food resources for this animal. From late summer to the following spring, acorns, hickory nuts, walnuts, and butternuts constitute much of the squirrel's diet. During the rest of the year, however, squirrels have been observed consuming wild fruits and berries (such as blackberries and strawberries), mushrooms, small ants, insects, birds, eggs, and at times, carrion (Shorten, 1954; MacClintock, 1970). Their most active feeding season is in autumn, when they build up a fatty layer of tissue to protect themselves during the approaching winter (Short and Duke, 1971). At this time, they may also be observed burying nuts, using their forearms to dig, for consumption during the winter (Nichols, 1927).

Locomotor Activities

The locomotor pattern of the grey squirrel is described as scansorial, that is, it scrambles up and down vertical surfaces quadrupedally. However, its movements are also of a type called <u>par</u> <u>saccades</u>, a rapid darting pattern which requires very rapid muscle movements (Murray, personal communication).

Upon descending a tree trunk, the grey squirrel comes head first with its body pressed flat against the bark and its legs spread out sideways. Its descents are jerky because it claws are used as hooks in holding the animal close to the trunk. Grey squirrels can be quite acrobatic in their locomotor behavioral repertoire. At times, when food becomes inaccessible by any other manner, the animals will hang head downward with their bodies braced against a vertical branch or tree secured only by the claws of the hindfeet allowing the forefeet to manipulate the food (Shorten, 1954). Running on the ground, squirrels have been clocked up to eighteen miles per hour; and, they are capable of leaping three to five feet with each thrust of their hindlimbs. While in their arboreal habitat, squirrels can leap a distance of twelve feet while jumping between the branches of two trees (Shorten, 1954). In an urban environment, a squirrel has been observed climbing up the side of a four story brick building to reach the roof (personal observation).

Postural Positions

Various postures typical of the grey squirrel's behavioral repertoire have been observed. Grey squirrels may be found sprawling, straddled on a branch sunning their backs on warm cloudless days (Shorten, 1954). Squirrels also sit on their haunches while eating an object held between their forepaws. The tail is very important in this posture as in other postures; it acts as a tripod to hold the animal in a stable position while sitting and is used as a balance while jumping, climbing, running along branches, and making quick turns (MacClintock, 1970).

Structure of the Manus

The forelimbs of the squirrel are important for reasons other than that they are essential in locomotion. They are necessary for obtaining food, and are used to a great extent as tactile receptors.

The forefeet of the squirrel retain the primitive pentadactyl condition; however, the pollex is greatly reduced and arises from the side of the inner carpal pad. The pollex has a nail rather than a claw as do the other four digits (Pocock, 1922). The claw, or falcula, is used for attack and defense, digging, or climbing. It is strongly compressed from side to side, and sharply curved and molded closely on the terminal phalanx of the digit (Le Gros Clark, 1936, 1959; Romer, 1970) (Plate 4).

Of the five digits of the manus, the fourth is the largest. The third and fourth digits are more closely united to each other at their base than they are to the second or fifth digits (Pocock, 1922).

A definite arrangement of walking or volar pads cover the palms of the squirrel's manus as well as the soles of the pedes. Ten elements can be distinguished on the walking pads of the manus: five apical pads, three interdigital pads, the thenar pad, and the hypothenar pads (Bryant, 1945). The apical pad of the pollex is the smallest. The radial, middle and ulnar interdigital pads are situated at the base of the digits 2, 3, 4, and 5. The thenar pad is larger and

Plate 4. Dorsal view of the manus of *Sciurus carolinensis*. (Measured in centimeters.)

more distally situated than the hypothenar. The pattern of the volar pads of the squirrel differ from the basic mammalian pattern of four interdigital pads. The number of the remaining pads, however, is identical (Biegert, 1971) (Plate 5). The function of these pads is to protect the deeper soft structures of the manus and act as shock absorbers when the skin would be pressed against the skeletal parts of the hand (Schultz, 1969).

The carpal vibrissae are important in the tactile perception of the grey squirrel. These vibrissae are situated on the forearms just proximal to the wrist and usually towards the inner side. The vibrissae are implanted by large bulbous roots in small cutaneous tubercles which are richly innervated. By making contact with objects in the immediate environment, or even from the air repulsed by the mere approach to a firm surface, these sensory hairs convey much information about the objects in the immediate environment. Thus, the carpal vibrissae of the squirrel are especially important for conveying information about the approach of a landing place during a leap, thus triggering the grasping reflex in the fingers (Le Gros Clark, 1959; Schultz, 1969).

Summary

Saimiri is found most often in large troops in the low canopy and the dense undergrowth of the forest margins where

Plate 5. Ventral view of the manus of <u>Sciurus carolinensis</u>. (Measured in centimeters.)

it feeds on fruits and insects. It is described as a branch running and walking quadruped with specializations of nails and friction ridges on its hands. Saimiri's fingers are capable of convergence and prehensility. This is important in many aspects of the animal's behavior including feeding and locomotion. In terms of locomotion, when a vertical support is small relative to the size of the animal, the hands can easily secure the grip needed to prevent it from falling. Where the support is large (such as the trunk of the tree), the grip must be secured by embracing the support with the forefeet and fixing the digits on either side of the support. The Saimiri manus is, therefore, more perfectly adapted for a fine, terminal branch setting, than a large vertical branch setting. In terms of feeding, prehensility is important in retrieving and eating in a terminal branch milieu.

Tupaia is a forest floor predator with a manus which is convergent, but not prehensile, and has claws and friction ridges on its digits. It is a generalized quadruped which employs rapid, scurrying movements in its locomotor activities. It is capable of fine acrobatic movements in a terminal branch setting, but it does not have the fine manual dexterity as does the squirrel monkey.

Sciurius is a herbivore which ranges vertically, foraging as much on the ground as in the trees. Its manus is clawed and it lacks friction ridges. Its fingers are neither convergent nor prehensile. The fingers' claws aid the animal in a vertical setting in that when the support is too large to be securely gripped, the claws can be dug into the support. Prehensility of the fingers is not needed in its arboreal feedings, since food items (such as fruits and buds) are bitten from the tree, and if dropped to the ground, can be retrieved for consumption on the ground.

CHAPTER V

PRACTICAL USE OF THE MANUS IN THE SQUIRREL MONKEY AND THE TREE SHREW

To determine the variations of use of the manus of the experimental animals, studies were performed to explore specific locomotor and manipulatory behavior of the squirrel monkey in order to compare it to similar research on the tree shrew (as presented by Bishop, 1964). Squirrels were not tested in the present experiments due to lack of adequate caging and testing facilities. A search of the literature has shown that similar research was not performed on these animals.

Dowel-Walking Experiment

The first experimental procedure performed was used to determine the animals' choice of hand orientation on dowels of various diameters. This study was performed by undertaking a photographic essay of the way the experimental animals position their manus along the long axis of the dowels. For each dowel, six squirrel monkeys were tested, ideally for seventy-six trials. As all seventy-six trials were not photographically legible, usable trials ranged from thirty-two to seventy-four in number. The monkeys were placed in a glass cage (1.8 m x 1.5 m x .9 m) which contained a single rod placed at a 45° angle. A 35 mm camera attached to a stationary platform placed beneath the rod was used to photograph the animals' manus while they were used by the animals in the act of locomotion. The dowels were varied in diameter (5 cm, 3.4 cm, 2 cm, and 1.25 cm) to demonstrate the change of orientation of the animals' manus related to the size of the dowel.

Records of the orientation of the hand on the dowels were obtained by drawing the long axis of the top of the branch on an outline of the animals' manus and scoring the number of times the animals used each orientation. Tables 2-5 list the percentage of times the axis of the various sized diameter dowels crossed each part of the manus. The scoring system used is that which was suggested by Bishop (1964). Comparison of data, therefore, will be facilitated by using an identical scoring system. Each score is counted in two places; the first describing where the axis initially crossed the manus, the second describing where the axis terminally crossed the manus. Therefore, an observation which showed that the axis fell from the hypothenar pad to the index finger is counted both as "Hth" and as "d2" ("Hth" indicating the hypothenar pad and "d2" indicating digit 2). The total count is thus 200 "percent".

Some particularly interesting grips can be noted in the count of 251 grips on a dowel 1.25 cm in diamter (placed at a 45° angle) (Table 2). Saimiri sciurius' manus fell with the axis of the dowel between digits 1 and 2 in 75.1 percent of the grips. The axis of the dowel fell through digit 5 in only .9 percent of the grips, and between digits 4 and 5 in none of the grips. In 26.9 percent of the grips, the dowel crossed the manus at a position greater than digit 5. In 62.1 percent of the grips, the dowel crossed the base of the palm rather than lying under or between any of the fingers.

In a count of 244 grips on a dowel 2 cm in diameter (placed at a 45° angle), some particularly interesting grips can be noted (Table 3). Saimiri sciurius' manus fell with the axis of the dowel between digits 1 and 2 in 58.2 percent of the grips. The axis of the dowel fell through digit 5 only 3 percent of the grips, and between digits 4 and 5 in none of the grips. In 41.2 percent of the grips, the dowel crossed the manus at a position greater than digit 5. In 44.4 percent of the grips, the dowel crossed the base of the palm rather than lying under or between any of the fingers. Plate 6 shows Saimiri in locomotion using the preferred grip on dowels 3.4 cm, 2 cm, 1.25 cm in diameter.

Some particularly interesting grips can be noted in a count of 306 grips on a dowel 3.4 cm in diameter (placed at a 45° angle) (Table 4). Saimiri sciurius' manus fell with

TABLE 2

ORIENTATION COUNT

Frequency in 200 percent those parts of the hand which fell on the long axis of the 1.25 cm dowel for <u>Saimiri sciurius</u>.

ANIMAL	GRIPS COUNTED	<d1	d1	d1-d2	d2	d2-d3	d3	d3-d4
Half Nose	66	3	18.2	75.8	0	1.5	1.5	3
Half Tail	53	7.5	13.2	79.2	5.7	1.9	0	0
Ma	58	6.9	20.7	72.4	0	1.7	0	0
Peak	74	14.9	29.7	73	1.4	1.4	1.4	0
Total	251							
AVERAGE		8.1	20.4	75.1	1.8	1.6	.7	.7

	d4	d4-d5	d5	>d5	BASE PALM	NO PART OF HAND
Half Nose	0	0	0	19.7	77.3	0
Half Tail	0	0	3.8	35.9	52.8	0
Ma	0	0	0	34.5	60.3	3.5
Peak	0	0	0	17.5	58.1	2.7
AVERAGE	0	0	.9	26.9	62.1	1.6

Legend:	d	Indicates digit
	1-5	Indicates the number of digits
	d-d	Indicates interdigital spaces
	<d1	Indicates the area from digit 1 to the base palm
	>d5	Indicates the area from digit 5 to the base palm

TABLE 3

ORIENTATION COUNT

Frequency in 200 percent those parts of the hand which fell on the long axis of the 2 cm dowel for _Saimiri_ _sciurius_.

ANIMAL	GRIPS COUNTED	< d1	d1	d1-d2	d2	d2-d3	d3	d3-d4
Rudy	52	5.8	34.6	57.7	1.9	3.8	0	0
Straight Nose	32	7.1	28.6	67.9	0	3.6	0	0
Half Nose	25	4	16	72	0	4	4	0
Half Tail	49	32	6	48	2	4	2	0
Ma	50	12	12	76	2	0	0	0
Peak	36	16.7	33.3	37.8	5.6	0	0	0
Total	244							
AVERAGE		12.9	21.8	58.2	1.9	2.6	1	0
Bishop's Data	60	75	2	13	2	0	2	2

	d4	d4-d5	d5	>d5	BASE PALM	NO PART OF HAND
Rudy	0	0	0	42.3	53.8	0
Straight Nose	0	0	0	42.9	50	0
Half Nose	0	0	4	20	52	16
Half Tail	2	0	2	78	12	12
Ma	0	0	4	36	54	4
Peak	2.8	0	8.3	27.8	44.4	33.3
AVERAGE	.8	0	3	41.2	44.4	10.9
Bishop's Data	2	2	5	66	29	0

Plate 6. Preferred orientation of the manus of Saimiri sciurius on 3.4 cm, 2 cm, and 1.25 cm diameter dowels as observed in the present experiments. Note that the long axis of the dowel lies most frequently on the interdigital space between digits 1 and 2 and on either the area between digit 5 and the base palm or the base palm itself. The monkey viewed here is on a 2 cm rod.

TABLE 4

ORIENTATION COUNT

Frequency in 200 percent those parts of the hand which fell on the long axis of the 3.4 cm dowel for <u>Saimiri</u> <u>sciurius</u>.

ANIMAL	GRIPS COUNTED	< d1	d1	d1-d2	d2	d2-d3	d3	d3-d4
Rudy	36	19.4	22.2	52.8	5.6	5.6	0	0
Straight Nose	52	26.9	11.5	59.6	0	1.9	0	0
Half Nose	54	31	7	54	6	4	2	2
Half Tail	63	22	16	46	4	4	4	4
Ma	52	6	12	82	0	0	0	0
Peak	49	8.2	10.2	79.6	0	0	0	0
Total	306							
AVERAGE		18.9	13.2	62.3	2.6	2.6	1	1

	d4	d4-d5	d5	> d5	BASE PALM	NO PART OF HAND
Rudy	0	0	0	72.2	22.2	0
Straight Nose	0	0	0	90.4	9.6	0
Half Nose	0	0	0	81	13	0
Half Tail	2	0	4	72	16	6
Ma	0	0	0	94	6	0
Peak	0	0	0	93.9	4.1	4.1
AVERAGE	.3	0	.6	83.9	11.8	1.7

the axis of the dowel between digits 1 and 2 in 62.3 percent of the grips. The axis of the dowel fell through digit 5 only .6 percent of the grips, and between digits 4 and 5 in none of the grips. In 83.9 percent of the grips, the dowel crossed the manus at a position greater than digit 5. In 11.8 percent of the grips, the dowel crossed the base of the palm rather than lying under or between any of the fingers.

In a count of 224 grips on a dowel 5 cm in diameter, (placed at a 45° angle), some particularly interesting grips can be noted (Table 5). Saimiri sciurius' manus fell with the axis of the dowel between the digits 1 and 2 in 18.9 percent of the grips. The axis of the dowel fell through digit 5 only 1.6 percent of the grips. In 4.7 percent of the grips, the dowel crossed the manus at a position greater than digit 5. In 37.7 percent of the grips, the dowel crossed the base of the palm rather than lying under or between any of the fingers. Plate 7 shows Saimiri in locomotion using the preferred grip on a dowel 5 cm in diameter.

In comparison, Bishop (1964) found that in a count of 60 grips on a dowel 2 cm in diameter, (angle of the dowel not noted), the manus of Saimiri sciurius' fell with the axis of the dowel between digits 1 and 2 in 13 percent of the grips (Table 3). The axis of the dowel fell through digit 5 in 5 percent of the grips, and between digits 4 and 5 in 2 percent of the grips. In 66 percent of the grips, the dowel

Plate 7. Preferred orientation of the manus of <u>Saimiri sciurius</u> on the 5 cm diameter dowel as observed in the present experiments. Note that the hand falls on either side of the long axis of the dowel rather than crossing it.

crossed the manus at a position greater than digit 5. In 29 percent of the grips, the dowel crossed the base of the palm rather than lying under or between any of the fingers.

Bishop (1964) also found that in a count of 62 grips on a dowel 5 cm in diameter (angle of the dowel not noted), *Saimiri sciurius*' manus fell with the axis of the dowel between digits 1 and 2 in 23 percent of the grips (Table 5). The axis of the dowel fell through digit 5 in none of the grips and between digits 4 and 5 in 2 percent of the grips. In 53 percent of the grips, the dowel crossed the base of the palm rather than lying under or between any of the fingers.

From these data, Bishop thus states the favored position of *Saimiri* on 2 cm diameter dowel is with the knuckles of digits 1 to 5 flexed around the dowel (Table 8). However, the data presented in this paper indicate that the favored position of *Saimiri* (on 3.4 cm or smaller diameter dowels) is the top axis of the dowel falling between d1 and d2. Therefore, d2, d3, d3 and d5 are flexed around one side of the dowel and d1 flexed around the other side of the dowel in opposition with the rest of the hand (Table 6).

There may be several explanations for the differences in the data. Bishop did not state at what angle, if any, she placed her dowels when noting the grips of the animals. Secondly, she did not note how the grips of the animals were observed. In the present study, a photographic record was

TABLE 5

ORIENTATION COUNT

Frequency in 200 percent those parts of the hand which fell on the long axis of the 5 cm dowel for <u>Saimiri sciurius</u>.

ANIMAL	GRIPS COUNTED	<d1	d1	d1-d2	d2	d2-d3	d3	d3-d4
Rudy	66	24.2	24.2	33.3	0	1.5	1.5	1.5
Half Tail	51	27.5	23.5	9.8	11.8	21.6	0	0
Ma	73	31.5	61.6	16.4	6.8	11	0	1.4
Peak	34	30.4	44.4	16	0	4	0	0
Total	224							
AVERAGE		28.4	38.4	18.9	4.7	9.5	.4	.7
Bishop's Data		53	0	23	11	0	8	3

	d4	d4-d5	d5	>d5	BASE PALM	NO PART OF HAND
Rudy	3	0	3	7.6	51.5	48.5
Half Tail	0	2	2	9.8	37.3	54.9
Ma	0	1.4	1.4	1.4	37	30.1
Peak	0	0	0	0	25	77.8
AVERAGE	.7	.8	1.6	4.7	37.7	52.8
Bishop's Data	0	2	0	53	47	0

Plate 8. Preferred orientation of the manus of Saimiri sciurius on the 2 cm and 5 cm diameter dowels as observed by Bishop (1964). Note that digits 1-5 are flexed around the dowel and the long axis of the dowel crosses less than digit 1 and either greater than digit 5 or the base palm. The monkey viewed here is on a 2 cm rod.

made of each grip to accurately preserve the orientations of that grip. Thirdly, Bishop's sample size was only one fourth as large as the present data noted for the two dowel sites she tested. Using a larger sample population, the data might have changed somewhat in my direction.

From the data currently presented, it can be noted that the squirrel monkey orients its hands on branches in sharply preferred positions. The monkey tends to hold on with d1 opposing d2, d3, d4, and d5 in flexion around the dowels with diameters of 1.25 cm, 3 cm and 3.4 cm. On the larger dowel of 5 cm diameter, this orientation was not as clear. The monkey tends to simply walk on top of the dowel rather than grasping it, and a greater variation in the preferred orientation of the grip is noted (Plates 6 and 7).

With Tupaia glis, in a count performed by Bishop (1962, 1964) of 243 grips on a horizontal dowel 0.6 cm in diameter, some particularly interesting grips can be noted (Table 6). The animal's manus fell with the axis of the dowel between digits 1 and 2 in 12 percent of the grips. The axis of the dowel fell through digit 5 in 14 percent of the grips, and between 4 and 5 in 28 percent of the grips. In only 4 percent of the grips the axis crossed the base of the palm rather than lying under or between any of the fingers.

The preferred orientation of the tree shrew as observed by Bishop is quite variable. The base of the palm

TABLE 6

ORIENTATION COUNT

Frequency in percent[1] that parts of the hand which fell on the long axis of horizontal dowel for <u>Tupaia glis</u>. (Bishop, 1964)

DIAMETER OF DOWEL	GRIPS COUNTED	< d1	d1	d1-d2	d2	d2-d3	d3
0.6 cm	243	20	2	12	2	6	2

d3-d4	d4	d4-d5	d5	> d5	HTH[2] PAD	CENTER PALM
8	6	28	14	18	16	24

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[1] Bishop's reported data add up to only 158 percent rather than 200 percent.

[2] Hth pad indicates the hypothenar pad.

is often not used alone. Of the grips which involve the digits, the most common oppose digits 1 to 4 on one side of the branch, to the large hypothenar pad on the other side. Digit 1 is not used often in opposition to digits 2 to 5 in Tupaia glis.

It is unfortunate that only a dowel of one size was used in Bishop's study since this offers no opportunity to study the variance of orientations with the variance in the size of the dowels.

Manual Dexterity Experiment

A second experimental procedure attempted to demonstrate the animals' dexterity in maneuvering and manipulating objects. Each of the six squirrel monkeys was placed in a box with one end covered by wire mesh (1.25 cm, 2.5 cm, and 5 cm squares). Sunflower seeds and slices of peanuts were placed at 1.25 cm intervals (beginning at 1.25 cm and reaching a length of 11.25 cm) from the mesh (Plate 9). Each animal was tested for 25 trials at each interval and was evaluated for the number of: (1) unsuccessful attempts, (2) attempts made with just touching the object, and (3) successful attempts made in obtaining the object. Tables 7 through 11 reflect the results of the experiment with Saimiri. In general, it can be seen that the animals were highly successful in retrieving the objects through the 2.5 cm and 5 cm square mesh when placed at varying distances

TABLE 7

ACCURACY TEST FOR *SAIMIRI SCIURIUS*

ANIMAL: RUDY

MESH SIZE	DISTANCE OF OBJECT FROM MESH	TOTAL ATTEMPTS	TOUCHED OBJECTS	SUCCESS IN OBTAINING OBJECT
1.25 cm	1.25 cm	25	11	13
	Animal refused object at any other distance from cage			
2.5 cm	1.25 cm	25	0	25
	3.75 cm	25	0	25
	6.25 cm	25	0	25
	8.75 cm	25	0	25
	11.25 cm	25	0	25
5 cm	1.25 cm	25	0	25
	3.75 cm	25	0	25
	6.25 cm	25	0	25
	8.75 cm	25	0	25
	11.25 cm	25	0	25

TABLE 8

ACCURACY TEST FOR *SAIMIRI SCIURIUS*

ANIMAL: HALF NOSE

MESH SIZE	DISTANCE OF OBJECT FROM MESH	TOTAL ATTEMPTS	OBJECTS	SUCCESS IN OBTAINING OBJECT
1.25 cm	1.25 cm	2	0	2
	Animal refused object at any other distance from cage			
2.5 cm	1.25 cm	25	0	25
	3.75 cm	25	0	25
	6.25 cm	25	0	25
	8.75 cm	25	0	25
	11.25 cm	25	0	25
5 cm	1.25 cm	25	0	25
	3.75 cm	25	0	25
	6.25 cm	25	0	25
	8.75 cm	25	0	25
	11.25 cm	25	0	25

TABLE 9

ACCURACY TEST FOR SAIMIRI SCIURIUS

ANIMAL: HALF TAIL

MESH SIZE	DISTANCE OF OBJECT FROM MESH	TOTAL ATTEMPTS	TOUCHED OBJECTS	SUCCESS IN OBTAINING OBJECT
1.25 cm	1.25 cm	25	0	25
	2.5 cm	4	2	2
	Animal refused object at any other distance from cage			
2.5 cm	1.25 cm	25	0	25
	3.75 cm	25	0	25
	6.25 cm	25	0	25
	8.75 cm	25	0	25
	11.25 cm	25	0	25
5 cm	1.25 cm	25	0	25
	3.75 cm	25	0	25
	6.25 cm	25	0	25
	8.75 cm	25	0	25
	11.25 cm	25	0	25

TABLE 10

ACCURACY TEST FOR SAIMIRI SCIURIUS

ANIMAL: MA

MESH SIZE	DISTANCE OF OBJECT FROM MESH	TOTAL ATTEMPTS	TOUCHED OBJECTS	SUCCESS IN OBTAINING OBJECT
1.25 cm	1.25 cm	25	2	23
	Animal refused object at any other distance from cage			
2.5 cm	1.25 cm	25	0	25
	3.75 cm	25	0	25
	6.25 cm	25	0	25
	8.75 cm	25	0	25
	11.25 cm	25	0	25
5 cm	1.25 cm	25	0	25
	3.75 cm	25	0	25
	6.25 cm	25	0	25
	8.75 cm	25	0	25
	11.25 cm	25	0	25

TABLE 11

ACCURACY TEST FOR *SAIMIRI SCIURIUS*

ANIMAL: PEAK

MESH SIZE	DISTANCE OF OBJECT FROM MESH	TOTAL ATTEMPTS	TOUCHED OBJECTS	SUCCESS IN OBTAINING OBJECT
1.25 cm	1.25 cm	25	8	17
	2.5 cm	5	0	1
	Animal refused object at any other distance from cage			
2.5 cm	1.25 cm	25	0	25
	3.75 cm	25	0	25
	6.25 cm	25	0	25
	8.75 cm	25	0	25
	11.25 cm	25	0	25
5 cm	1.25 cm	25	0	25
	3.75 cm	25	0	25
	6.25 cm	25	0	25
	8.75 cm	25	0	25
	11.25 cm	25	0	25

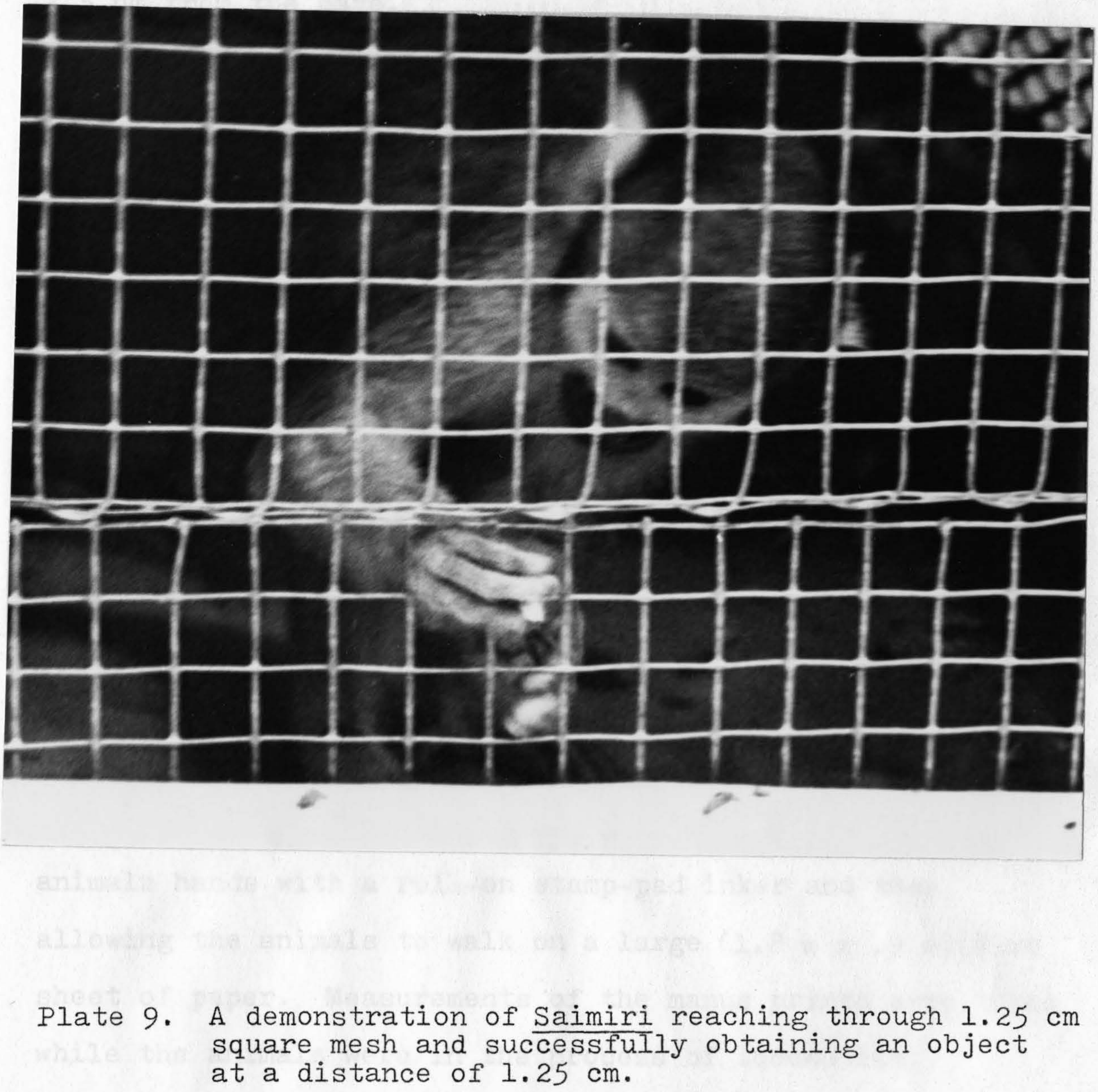

Plate 9. A demonstration of Saimiri reaching through 1.25 cm square mesh and successfully obtaining an object at a distance of 1.25 cm.

(up to 11.25 cm) from the cage. However, success varied with the 1.25 cm square mesh, and the majority of the animals refused to attempt to retrieve the object if placed over 2.5 cm from the cage.

Bishop (1964) ran a similar experiment with Tupaia, however, using mesh sizes of 1.25 cm, 1.88 cm, and 2.5 cm (due to the smaller size of Tupaia). The distances she used to separate the objects from the mesh were 1.25 cm, 2.5 cm, and 3.75 cm. Bishop observed a very low number of successes to touches. It can be noted that the number of successes decreased with the size of the mesh used. Table 12 reflects the results of the experiment with Tupaia.

The data thus show the squirrel monkey to be more dextrous in retrieving objects through various openings than the tree shrew.

Measurement of Handprints

The final experimental procedure involved taking handprints of the six individual squirrel monkeys by inking the animals hands with a roll-on stamp-pad inker and then allowing the animals to walk on a large (1.8 m x .9 m) flat sheet of paper. Measurements of the manus prints were taken while the animals were in the process of locomotion. (Plate 10) Table 13 gives a summary of the measurements of the handprints of both Saimiri and Tupaia. (Tupaia measurements were collected by Bishop (1964).

TABLE 12

ACCURACY TEST FOR *TUPAIA GLIS*
(Bishop, 1964)

MESH SIZE	TOTAL ATTEMPTS	TOUCHED OBJECTS	SUCCESS IN OBTAINING OBJECTS
1.25 cm	6	2	0
1.88 cm	13	2	7
2.5 cm	10	3	7

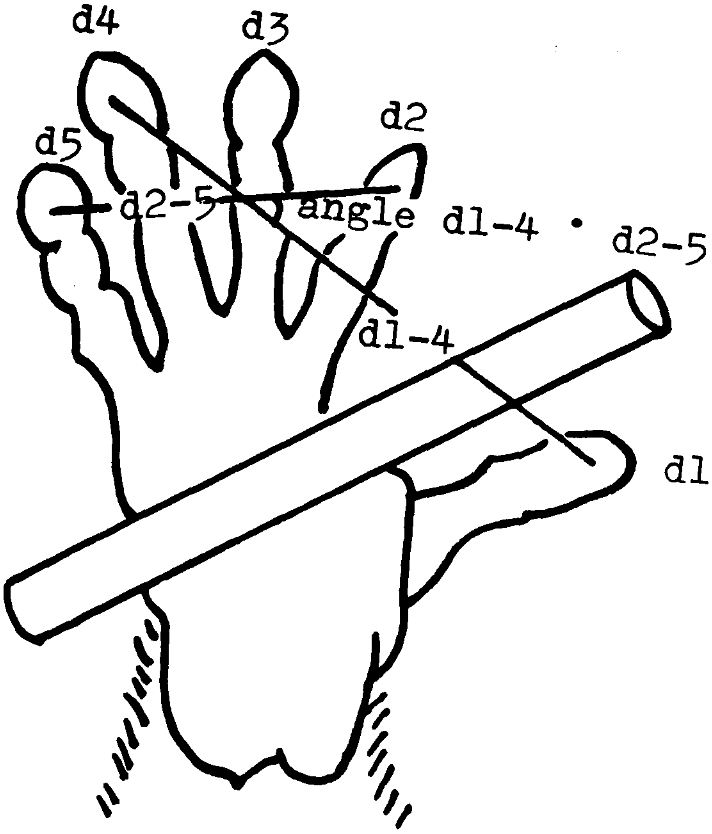

Plate 10. Demonstration of handprint measures for Tupaia and Saimiri. (Modified after Bishop, 1964)

TABLE 13

MEANS OF HANDPRINT MEASURES ON A FLAT SURFACE

Species: Saimiri sciurius

ANIMAL	EFFECTIVE GRASP (d1-4)	SPREAD OF REMAINING DIGITS (d2-5)	RELATIVE DIVERGENCE OF THUMB (d1-4/d2-5)	MEASURE OF GRASP TO SPREAD (MEASURE SHAPE OF HAND) (d1-4:d2-5)
Half Tail	3.59 cm	3.47 cm	1.03	51.9°
Half Nose	3.36 cm	2.41 cm	1.39	53.3°
Peak	3.62 cm	3.23 cm	1.12	50.2°
Rudy	3.69 cm	3.04 cm	1.21	52.0°
Ma	3.72 cm	3.24 cm	1.15	60.0°
Species: Tupaia glis (Bishop, 1964)				
Female	1.4 cm	1.2 cm	1.1	58°
Male	1.4 cm	1.3 cm	1.1	62°

Legend:

d1-4	Measures the distance between the center of the touchpads of digits 1-4.
d2-5	Measures the distance between the center of the touchpads of digits 2-5.
d1-4/ d2-5	Is the ratio of d1-4 to d2-5.
d1-4: d2-5	Is the angle formed by the crossing of d1-4 and d2-5.

It can be seen from these results that Saimiri has a larger effective grasp (d1-4) and spread (d2-5) of the digits than does Tupaia. However, the relative divergence of the thumb (d1-4/d2-5) is approximately the same. It is interesting to note that the angle of grasp to spread (a measure of the shape of the hand) (d1-4:d2-5) is found to be smaller in Saimiri than in Tupaia.

Summary

From the presented data, it can be seen that Saimiri preferred a prehensile grip in the process of locomotion. The present data is in opposition to the data presented by Bishop (1964). She had reported a preferred grip in which all digits of the manus were flexed together on the same side of the dowel.

There is no preferred orientation of Tupaia, on the other hand. What was noted was that the hypothenar pad was often used in opposition to digits 1-4.

In terms of manual dexterity, the squirrel monkey has been proven to be much more dextrous than the tree shrew in reaching through small openings and obtaining objects.

Handprint measurements of Tupaia and Saimiri demonstrate that Saimiri's manus is smaller than Tupaia's, however, the relative divergence is the same.

CHAPTER VI

DISCUSSION

At present, there is a controversy about why the primates have retained specific characteristics such as an enlargement of the brain, a reduction of olfaction, visual field overlap, and grasping specializations of the cheiridia. The primates' retention of primitive mammalian traits, (the lack of specialization) has been attributed to their arboreal habitat. This is the premise that has been generally assumed by most students studying primate morphology and evolution.

In his arboreal theory of primates, Jones states that the primates retained the generalized arboreal characteristics of a basal, arboreal mammalian stock from which they evolved because they retained the arboreal habit. Through time, the primates refined these characteristics to fit the particular niches which they inhabit today. According to Jones, the reason why other arboreal mammalian orders, including rodents, have not retained these characteristics is because at some time in their phylogenetic history, they descended to the ground to become terrestrial for a period. By the time they once again ascended into the trees, they had lost the generalized arboreal features. Napier and Napier (1967) modified Jones' arboreal theory by stating that it is not enough that the primates have taken to an arboreal habit; the fact is, that they have taken to a specialized, unique arboreal habit. Cartmill (1970, 1972, 1974a, 1974b) in further refining the arboreal theory, postulates that the primate characteristics are indeed due to a specialized arboreal niche -- a fine, terminal branch habitat. It was in this habitat, Cartmill states, that the early insectivores had to refine their locomotor and feeding abilities in order to survive. (Refer to Chapter I for a more detailed review of the arboreal theories.)

In order to elucidate the problem of determining the reason for the primates generalized characteristics, both Jones' arboreal theory, and Cartmill's modified arboreal theory should be tested.

Studies have been undertaken within the present paper to test the validity of whether the original arboreal theory (which hypothesizes that the primates characteristics are adaptations to an arboreal habit) or the revised theory (which hypothesizes the primates' characteristics are an adaptation to a fine, terminal branch habitat). The squirrel monkey has been used as the model of the primates, the grey squirrel as a model of other arboreal mammals, and the tree shrew as a model of the transition between the arboreal mammals and primates in this paper.

Key points in Jones' theory are that: (1) primates have retained their primitive mammalian features because they evolved from primitive placental mammals who were arboreal in their habitat; and, (2) primates have retained the arboreal habit continuously throughout their arboreal history while the other arboreal mammals have not.

An investigation of the early paleontological history of the experimental animals has revealed that the early placental mammals' skeletal remains do not demonstrate the specializations of the hands and feet which are characteristic of many arboreal mammals. From these conclusions, it appears more probable from the skeletal remains of the early placental mammals that they were terrestrial in habit. This is, therefore, a negation of one of the key points presented by Jones in his arboreal theory.

The paleontological history of the squirrel monkey shows that the earliest known primate ancestors (widely accepted by paleontologists), the plesiadapids, were lemur-like prosimians. An analysis of the climatic conditions which were present when these animals existed has shown that the area in which the animal lived was covered with a tropical angiosperm forest. Examinations of these animals' molar patterns have led to the conclusion that the animals' dentition was adapted to a herbivorous-frugivorous diet. It may be concluded, therefore, that the earliest of primates were probably arboreal since, in the tropical forests, seed and leaf eating activities usually occur away from the ground. This assumption is supported by the analysis of the skeletal remains which also indicates that the animals were arboreal in habit. There is no indication in the fossil remains of the squirrel monkey to indicate that this animal was terrestrial in habit at any time. The lack of fossil remains of the primitive Ceboidea in later periods, in the western United States and Central America, may be an indication that the gradual cooling trend which was occurring during that period gradually caused the extinction of the tropical forests which existed earlier and thus the inability of these animals to exist in the cooler, non-tropical forest areas. Fossil Ceboidea have been found only in paleontological remains which indicated the existence of tropical forests. This may be an indication of the continued arboreality of the animals.

In the case of the tree shrew, while the present-day morphology of this animal resembles the skeletal remains of the plesiadapids, there is no evidence to indicate a phylogenetic relation between these animals. Until the uncertainty regarding the phylogeny of the tupaiids has been lifted, it will be impossible to discover the arboreal or the non-arboreal ancestry of *Tupaia glis*.

The paleontological history of the grey squirrel indicates that one of the earliest ancestors of the squirrels may be the plesiadapids which, as stated previously, was considered to be arboreal. As the question of a direct line between these animals is under discussion, it cannot be specifically stated that the squirrel evolved through an arboreal ancestry. The earliest fossil rodents, the paramyids, were rather unspecialized and their skeletal remains show no specific structural adaptations to indicate either a terrestrial or arboreal habitat. Oligocene members of the squirrel family have been proven to be arboreal in a climatic environment which produced a mixed deciduous forest.

Thus, in all three cases, the paleontologic study of the model animals has not proven the animals to be arboreal throughout their evolutionary history. However, there is also no evidence to indicate that the animals (except for their earliest mammalian forms) were ever terrestrial in habitat at any period in their evolutionary history.

An investigation of the behavioral aspects of the use of the manus of the experimental animals has aided in testing the validity of Cartmill's suggestion that the primates' characteristics had evolved due to an adaptation to environmental pressures brought on in a fine, terminal branch habitat.

A study of the recent behavioral patterns of the squirrel monkey indicates that the activity peak of the monkeys' is in early to midmorning when they can be found in the top of the canopy of the forest. It is in this activity peak that much of their foraging for food occurs. A study of the ecology of the rain forest has shown that the upper storey of the rain forest (in which the canopy is located) forms a discontinuous or open strata. The importance of this layer for the squirrel monkey is that the maximum density of fruits and leaves tends to be found on the periphery of the limbs far away from the trunk. The squirrel monkey, in order to reach a major source of its food resources must, therefore, be able to maneuver on the terminal branches of 120 to 150+ foot trees.

A second important factor found in the behavior of the squirrel monkey, is that another food resource is insects which are caught by hand and placed into the mouth. A fine precision grip is needed to capture insects by hand.

An important factor in the environment of the squirrel monkey is the preponderance of lianas in the various storeys of the trees which form a vast network among the trees. These lianas are used in conjunction with the trees as the surfaces used in locomotion. Again, this is an indication of use of the manus in a fine, terminal branch rather than broad branch environment.

It can be noted that the volar pads of _Saimiri_ are covered with dermatoglyphic friction ridges which project into the small concavities of the surface on which it is walking. Friction is, therefore, increased between the surface substrate and the manus which increases the ability of the monkey to cling to very small vertical branches (Cartmill, 1974b).

The orientation count of preferred grips as demonstrated in the present data shows a preference of a prehensile grip around the dowels 3.4 cm or smaller in diameter. However, such a preference was not noted in the 5 cm dowel.

In terms of dexterity of hand manipulation, experimental data showed the monkeys to have a much greater dexterity in reaching for and obtaining objects than the tree shrew which would correlate with their manipulative behavior manifested during feeding, that is, one-handed prehensile grasping.

An investigation of the tree shrew's behavioral pattern shows that a precision grip of the manus is not used in feeding. The tree shrew is considered to be an arboreal forest-floor predator (Cartmill, 1972), that is, its major food resources are invertebrates concealed in the detritus of the forest floor. Insects are not caught in the hand, but rather are trapped beneath the forefeet and eaten while held in this position. A convergent and divergent hand is very well adapted to this kind of capturing and eating insects.

The tree shrew's manipulative ability in Bishop's experimental procedure has shown it to have little fine hand control which would correlate with its lack of prehensile grip as noted in its feeding behavior.

Bishop's data (1964) of the preferred orientation of the hand on a 0.6 cm dowel has shown that Tupaia glis lacks a clearly defined manual grip pattern. However, in Bishop's observations, the manus was almost always positioned across the branch in such a way that the branch lay between some of the digits and the hypothenar pad. The hypothenar pad is thought, therefore, to oppose digital flexion, with the result that the manus is capable of adapting to, if not actively gripping a cylindrical substrate (Jenkins, 1974). This would, therefore, be a great aid in adapting to a forest floor environment which is covered with roots and littered with plant debris.

The behavior of the grey squirrel is indicative of its adaptation as a vertical climber. The grey squirrel is well adapted to not only a vertical substrate, but also is equally well adapted to running along horizontal supports, hanging beneath slender supports, leaping from tree to tree, and many other arboreal locomotor activities which were previously thought to be only possible with terminal digit pads ". . . which provide a much more efficient grasping mechanism for animals which find it necessary to indulge in arboreal acrobatics" (Le Gros Clark, 1959: 174).

Although squirrels can move and forage among the terminal branches of the canopy and shrub layer, they spend little time actually feeding there. The squirrel will ordinarily bite loose a food item from a slender branch and then retreat with it to a larger branch or trunk to feed, or drop it to the ground to be eaten later (Shorten, 1954). Thus, while the grey squirrel is capable of terminal branch maneuvering, it is not comfortable doing so.

On the other hand, Cartmill (1974b) has stated that the clawed digits of the arboreal mammals are superior to the friction ridges of the primates on large vertical supports by embedding the claw into the substrate surface, thereby combatting the gravitational forces working against the animal.

From the behavioral data, it appears that each of the individual morphological, functional and behavioral aspects of the hands of the experimental animals are related to their specific environment. Thus, this is an indication towards an affirmation of the revised arboreal theory, i.e., that the primates' characteristics (specifically the structure of the manus as presented in this study) is the result of an adaptation to a fine, terminal branch environment.

Summary

The characteristics of primates, such as the reduction of the snout and olfactory sense, convergent eye orbitals, enlargement of the brain, greater manipulatory functions of the cheridia, etc., have been explained by most physical anthropoligists as adaptations to a general arboreal habitat. As one of the earliest proponents of this explanation, F. Wood Jones stated in his arboreal theory of primates that the primates, whom he believed had evolved from an arboreal basal mammalian stock, retained the generalized arboreal characteristics of these early mammals because they retained the arboreal habit. Through time, the primates refined these characteristics to fit the particular niches which they inhabit today. According to Jones, the reason other arboreal mammalian orders, including rodents, have not retained these characteristics is because at some time in their phylogenetic history, they descended to the ground to become terrestrial for a period. By the time they once again ascended into the trees, they had lost the generalized arboreal features. Napier and Napier modified Jones' arboreal theory by stating that it is not enough that the primates have taken to an arboreal habit; the fact is that they have taken to a specialized unique arboreal habit. Cartmill, in further redefining the arboreal theory, postulates that the primate characteristics are indeed due to a specialized arboreal niche, a fine terminal branch habitat. It was in this habitat that the early insectivores had to refine their locomotor and feeding abilities in order to survive. Tree shrews serve as useful models of these insectivores.

It was beyond the scope of this study to focus on all ten orders of arboreal mammals and compare them with the primate order. Instead, a partial elucidation of this problem has been reached through library research on the paleontological, environmental, and behavioral differences of the squirrel monkey (as a representative of the arboreal primates), of the tree shrew (as representative of the transition between the arboreal primates and arboreal mammals), and the grey squirrel (as representative of the arboreal mammals).

The earliest mammals were nocturnal foragers who for the most part were terrestrial rather than arboreal in habitat. A primate close to the basal ancestor of both modern primates and rodents, Plesiadapis, however, is thought to be arboreal. The limited paleontological history of the squirrel monkey suggests that this species appears to be exclusively arboreal throughout its history. The paleontological history of the tree shrew is too limited to establish the arboreality of the tree shrew lineage. The paleontological history of the squirrel, while not demonstrating that the species was exclusively arboreal (due to a fragmentary fossil record), shows that there is no evidence that the ancestral squirrels were terrestrial at some point in time. This evidence negates Jones' theory.

The ecological habitat of all three modern species are forestrial with the squirrel monkey and the tree shrew residing in tropical rain forests and the grey squirrel residing in a temperate deciduous forest. In terms of locomotor activities, the squirrel monkey is described as being a branch running and walking quadruped; the tree shrew is described as an arboreal and forest floor quadruped who employs rapid, jerky, scurrying movements (rather like a squirrel); and the squirrel is described as being a vertical climber.

The differences of these adaptive niches may be reflected in part in the differential anatomy of the manus of the animals. The monkey terminates its digits with nails, and has a prehensile hand with quite indistinct volar pads, and with specializations of papillary ridges which function as sensitive tactile receptors. The manus of the tree shrew terminates its digits with claws, and has very distinct volar pads. The fingers of the tree shrew are able to converge but are incapable of truly prehensile behavior. The squirrel is known to have claws terminating its digits, a definite arrangement of volar pads on its palms, and carpal vibrissae on the forearm proximal to the wrist.

The structural differentiation of the hands of these animals seems to also be correlated with their food gathering activities in that the squirrel monkey's hand is used to grasp and hold food with a prehensile grip while this is not required by the tree shrew and the grey squirrel.

In determining how the animals actually use their hands, an orientation count of the preferred grips of the manus on various sized dowels was made. These studies indicates that the squirrel monkey prefers to use a prehensile grip (that is digit 1 opposed digits 2 to 5) on dowels 3.4 cm in diameter or smaller. This is in contradiction of Bishop's (1964) data, which indicates that all digits of the hand were flexed in same direction on the same side of the dowel. The tree shrew is reported by Bishop not to have a clearly defined grip pattern.

In terms of manual dexterity, the squirrel monkey demonstrates great dexterity in reaching for and obtaining small objects. The tree shrew as reported by Bishop, lacks this manipulative ability.

As determined by handprint measurements, the squirrel monkey has a smaller hand than the tree shrew. The relative divergence of the digits of both animals is approximately the same.

The differential structure of these hands appears also to indicate that while all three species are arboreal, the squirrel with its clawed cheiridia is suited to locomotor abilities of vertical tree trunk climbing, the tree shrew with its clawed cheiridia is suited to locomotor abilities of a scurrying, forest floor arboreal quadruped, and the squirrel monkey with its prehensile hands in adapted to locomotor abilities of fine terminal branch environment of the canopy of the rain forest. These data are an affirmation of Cartmill's revised arboreal theory of primate evolution.

Even though the data presented in this paper is an affirmation of the revised arboreal theory, it is in itself only an elucidation of the problem presented in this thesis. In order to fully prove either theory, studies should be undertaken (such as the present study) with each of the arboreal orders of mammals and compare them to the primate order. Only a specific and detailed study of each arboreal mammalian order can truly prove which arboreal theory is correct.

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The final copies have been examined by the director of the thesis and the signature which appears below verifies the fact that any necessary changes have been incorporated and that the thesis is now given final approval by the Committee with reference to content and form.

The thesis is therefore accepted in partial fulfillment of the requirements for the degree of Master of Arts.

April 24, 1978
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