ABSTRACT

REVIEW OF
THE PHYLOGENETIC POSITION
OF THE TREE SHREW
(TUPAIA GLIS DIARD),
WITH NEW OBSERVATIONS
ON THE
ARTERIA CAROTIS INTERNA

by Erla Anne Steuerwald

This study was made to evaluate all available evidence, including that provided by the branching pattern and distribution of the internal carotid arterial system, to determine the problematical phylogenetic position of the tree shrews (family Tupaiidae).

Arteries of the cranial region of *Tupaia glis* Diard were perfused with colored latex or silicone-rubber injection mass prior to dissection.

The observations indicated that the internal carotid arterial pattern of *Tupaia glis* is as primitive as that of any mammal, including monotremes and marsupials. *Tupaia glis* deviates very little from the early post-branchial embryological pattern found in all mammals studied. The following features are regarded as primitive:

1. The branching pattern of the aortic arch is nearly symmetrical, typically displaying a left, as well as a right, brachiocephalic trunk.
2. The lingual artery is still the major branch of the external carotid stem. Facial and superficial temporal arteries are not well developed.
3. The pterygoid portion of the maxillary artery passes through an external alisphenoid canal.
4. The promontory (cerebral carotid) branch is as well developed as the stapedial branch of the internal carotid stem; both are of considerable diameter. (This observation conflicts with all previously published observations on Tupaiidae.)
5. The superior ramus of the stapedial artery is well developed, retaining continuity with its meningeal and orbital ramifications.
6. The proximal inferior ramus of the stapedial artery is usually present but attenuated.
7. Ethmoidal rami of the infraorbital, supraorbital, and intracranial anterior cerebral arteries all remain well developed; thus the latter vessel still reaches the nasal septum by way of the ethmoidal rete lying within the dura mater on the lamina cribrosa.
8. A transverse anterior communicating artery gives rise to a common anterior cerebral artery that bifurcates dorsal to the corpus callosum.

9. The bifurcation of the basilar artery usually produces a common stem, on each side, for the superior cerebellar and mesencephalic arteries.
10. The posterior cerebral and mesencephalic branches of the internal carotid-basilar anastomosis (posterior communicating artery) arise independently and still display a fairly metameric arrangement.

Peculiarities of the carotid branching pattern of *Tupaia glis* that are difficult to evaluate from a phylogenetic point of view include the following:

1. The orbital ramus of the infraorbital artery joins the ethmoidal branch of the superior ramus of the stapedial artery in the orbit.
2. The internal carotid and vertebro-basilar systems appear to share more or less equally in supply of the brain.
3. The true ophthalmic artery (branch of the cranial ramus of the cerebral carotid artery) is exceedingly reduced in calibre and joins the ciliary trunk arising from the stapedial artery (superior ramus).

Comparisons of the above-described features with Recent Primates and Insectivora indicate that Tupaiidae are generally more primitive than either, with no clear-cut indications of primate trends.

Review of the literature on all other known features of tupaiids indicates an essentially primitive mammalian status, with a considerable degree of resemblance to marsupials. The numerous similarities with Primates are probably the result of two factors: 1) parallel adaptation to an arboreal way of life and 2) derivation from a common ancestral stock with similar genetic potentialities for change.

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Erla Anne Steuerwald

A THESIS

Submitted to

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The funds needed for purchase of animals and materials were provided by a grant (GM 12635) to Dr. Daris R. Swindler from the National Library of Medicine, National Institutes of Health, Bethesda, Maryland.

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INTRODUCTION

In the earliest published sketch and description of tree shrews by Ellis in 1782, they were referred to as "squirrels" (Sciurus dissimilis), probably due to their arboreal habitat and feathery tails (Lyon, 1913).

That tree shrews were early regarded as members of the order Insectivora is evidenced by Diard's naming of a species as Sorex glis, in 1820. In 1822, the name Tupaia was proposed by Raffles for the genus that included the above-named species and two others. It was common practice among Europeans at that time to call these animals insectivores (Lyon, 1913). This may have been based on their variably insectivorous habits, dentition, pointed snouts, and high level of physical activity.

During the nineteenth century additional genera and species were described within the family Tupaiidae (Lyon, 1913). By 1884, Leche (as cited by Gregory, 1910) had decided that the families Tupaiidae and Macroscelididae (elephant shrews) were so widely separated from other Insectivora as to constitute a distinct order Menotyphla. Haeckel, in 1866 (cited by Simpson, 1945), established a more lasting precedent by considering Menotyphla as a suborder, with Lipotyphla (all other insectivores) as the second suborder, of the order Insectivora.

Gregory (1910), although proposing that Menotyphla constitute a distinct order, indicated a trend toward consideration of tupaiids as morphologically annectent forms between the order Insectivora and Lemuroidea (of the order Primates). Although these two groups may have separated very early, developing in parallel under the stimulus of similar arboreal habits, they still show true generic relationship.

Carlsson (1922) and Le Gros Clark (1925, 1926a, 1959) went even further, on the basis of morphological evidence, to place the superfamilies Tupaioidea and Lemuroidea within the suborder Prosimii of the order Primates.

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Straus (1949) and Martin (1966) would have established Tupaioidea as a separate order.

Recent evidence based on skull development, fossil teeth, central nervous system structure, and fetal membrane morphogenesis has tended to reverse this trend. Romer (1966) considered the family Tupaiidae as the only living representatives of the superfamily Leptictoidea, suborder Proteutheria, order Insectivora. Romer (1966) emphasized that it is very difficult to trace phylogenetic lines among the primitive eutherian mammals of late Cretaceous and Paleocene times. Often there are only fragmentary remnants of dentition. Groups that later became quite divergent were then very similar and closely related. All placental mammals of the late Cretaceous period might well be placed in a single family; and even in the Paleocene epoch, within a common order (Insectivora).

The order Insectivora includes not only the modern, variably adapted types but also the basic eutherian stock from which all modern eutherian types have evolved. The family Leptictidae is the basal stock from which most later, and all modern, placental mammals have been derived, according to the currently prevalent view among paleontologists (Romer, 1966).

On this view, the problem becomes one of determining the proximity of the basic primate and tupaiid stocks to their leptictoid forebears. To what extent do similarities among anthropoids, lemuroids, and tupaiids represent parallelism, convergence, or lineal ancestry? Nor are these evolutionary patterns mutually exclusive. By definition, <u>parallelism</u> is "the evolution of related organisms along similar lines so that they develop similar adaptations." It is to be distinguished from <u>convergence</u>, which is "the like response of quite unrelated organisms to like ecologic opportunities." (Definitions are quoted from Colbert, 1949.) Pertinent to the phenomenon of convergence is the observation that "the <u>directions</u> of possible mutations are not perfectly <u>ad libitum</u> but are limited to changes in such directions as can find expression in the gene complex actually at hand" (Jepsen, 1949).

The purpose of the present study is two-fold. First, since an organism adapts to its environment as a functioning whole, the literature on the various facets of tupaiid adaptation is reviewed. Second, since a gross anatomical study of the internal carotid arterial system of a tree shrew has apparently never been published, results of such a laboratory project on <u>Tupaia glis</u> are reported here in phylogenetic perspective.

REVIEW OF THE LITERATURE

Since there are no unquestioned tupaiid fossils, evidence regarding the phylogenetic position of this family may well be supplemented by less direct lines of evidence (van Valen, 1965; McKenna, 1966; Szalay, 1968).

The tree shrew resembles the primitive placental mammal as closely as any animal alive today. Since different functional systems evolve at differing rates, some features remain more generalized than others.

The genetic features and geographic distribution of Tupaiidae provide a theoretical basis for considerable speciation in the face of a fundamental conservatism of structure.

Geographic Distribution

Tree shrews range, geographically, from eastern India on the west, to Palawar (Philippine Islands) on the east; from southern China on the north, southward to Java and many small islands off the southwestern coast of Sumatra. No single genus exists throughout this range (Lyon, 1913; Buettner-Janusch, 1966). Since possible tupaiid fossils remain questionable, the significance of their Paleocene to Eocene distribution in Europe (*Messelina* and *Adapisoriculus*) and Mongolia (*Anagale*) cannot now be interpreted (van Valen, 1965; Romer, 1966; Szalay, 1968).

Genetic Features

Observation of tupaiid chromosome complements shows a high proportion of acrocentric chromosomes, indicative of a generalized condition (Bender and Chu, 1963; Klinger, 1963). There appears to be chromosomal polymorphism or even speciation among morphologically similar members of a species, such as *Tupaia glis* (Bender and Chu, 1963; Egozcue, Chiarelli, Sarti-Chiarelli, and Hagemenas, 1968). Any viable variants would probably have a better chance of perpetuating themselves in the small, isolated populations so prevalent among tupaiids. Buettner-Janusch (1966) pointed out that such "mutual isolation will have emphasized tendencies toward divergence."

In discussion of his isoimmunization theory, Goodman (1963) stated, however, that the possible acquisition of a hemochorial placenta by tupaiids would have tended to reduce their genetic plasticity, at least during the period of gestation (of approximately forty-five to sixty days).

Behavior

Patterns of behavior observed among Tupaiidae correlate well with other data used to speculate on phylogenetic position.

The "resting attitude" of *Tupaia glis* resembles that of primates with bushy tails. The tail is frequently brought forward alongside the body (Andrew, 1964).

Tupaia displays special behavior patterns for cleaning the face, especially after eating. Similar patterns are observed in most small mammals with generalized limbs, such as Macroscelididae (elephant shrews) and Sciuridae (squirrels). This specialized movement has never been observed in *Galago*, *Loris*, or *Lemur* (Andrew, 1964).

Regarding the source of facial expression, it has been suggested that the major primitive function of facial muscles was movement of vibrissae. Andrew (1964) noted that although vibrissal movement is rather extensively used for environmental scanning in rodents and in such insectivores as elephant shrews, it is absent in *Tupaia* and prosimians except as incidental to other facial movements. This may possibly be due to descent from a *Sorex*-like ancestor in which the entire snout was continually moved from side to side during exploration. In such a situation, independent movement of vibrissae would only make tactile data more difficult to interpret.

Andrew (1964) pointed out that although Urogale (Philippine tree shrew) has stereoscopic overlap of fifty to sixty degrees, it may not actually use such vision to any appreciable degree. Observation of Tupaia shows that the animal looks frontally in curiosity but generally uses monocular vision. All primates, including Galago and Lemur, use stereoscopic vision almost all the time. Andrew (1964) also noted that reduction of the muzzle is seemingly not correlated with acquisition of stereoscopic vision. Simons (1962) traced the known phylogeny of stereoscopic vision in fossil Primates. Plesiadapis (the oldest primate skull described to date), although lacking a postorbital bar, closely resembles modern tree shrews in the lateral direction of the orbits.

There is no high correlation between color vision and advanced stereoscopic vision among primates (Andrew, 1964). Tree shrews (Tupaia glis) display effective color vision (von Tigges, 1963, 1964; Noback and Shriver, 1967).

Insectivorous forms make less specialized use of the incisor teeth than do most mammals. The incisors may seize or tear, but the longer canines are better suited to such tasks. In the absence of cheeks, even premolars or molars may be so used. Since the incisors are not essential to feeding, it has been possible for them to become procumbent and specialized for grooming in Tupaiidae. In Lemuroidea and Lorisidae the procumbent incisors have become solely related to grooming, with important socializing consequences (Andrew, 1964). Simons (1962) cited evidence from both fossil and living prosimians and tupaiids that this tooth-scraper has arisen by parallelism in at least three stocks.

Tupaias may invent rather complex motor play, although showing a strong propensity for stereotyped activity (Vandenbergh, 1963; Kaufmann, 1965; Sorenson and Conaway, 1966).

No living Primates observed (including Tupaiidae) are as solitary as Insectivora. The degree of sociability observed by Andrew (1964) among tupaias (Tupaia glis) is greater than that among rats and mice. It contrasts more markedly with the intolerance displayed among elephant shrews (Macroscelididae). The solitary habits of the latter resemble those of most other insectivores.

Size and pattern of social groups varies somewhat among Tupaia species (Sorenson and Conaway, 1966). Lorisid societies are at a level of organization similar to those of Tupaiidae. Galago crassicaudatus is in some ways less social than Tupaia. With respect to mutual grooming, however, Andrew (1964) observed that both Galago and Perodicticus (potto) show greater sociability. Although this behavior is rare in most Tupaia species, males of all species attempt to groom females whenever the latter near estrus (Sorenson and Conaway, 1966). Tupaia longipes (Sorenson and Conaway, 1966) displays a social pattern that includes female-female consorts. Consorting females groom each other daily. Microcebus (mouse lemur), in rarely displaying mutual grooming behavior, is not far from a tupaia-like condition. Lemuroids, especially the diurnal species, tend to be more social than lorises (Andrew, 1964).

Sprankel (1961) described a form of scent signal called "urine washing." Andrew (1964), however, found the tupaias' behavior a bit "too unspecific in form" to homologize it. A somewhat similar behavior pattern occurs during courtship in Microcebus (Andrew, 1964).

Scent marking by means of cutaneous gland secretions is shared by Tupaia and Lemuroidea with some insectivores (Soricidae and Solenodon). Since the males of the insectivore and Lemur species have flank glands, while Tupaia bears its odoriferous glands on chin and throat, the movements by which the scent is applied to the female during courtship must also have evolved separately in Tupaiidae (Sprankel, 1961; Andrew, 1964).

Copulation patterns in Tupaia glis resemble those of Galago crassicaudatus in a number of ways (Andrew, 1964).

Martin (1966) observed the very unusual breeding behavior displayed by Tupaia (species not indicated). The male is entirely responsible for nest-building activity. This is unique among mammals. The female suckles the young only once every two days. Long intervals between brief suckling visits by the mother have also been observed in rabbits (Lagomorpha).

Young tupaias grow rapidly, reaching adult size by the age of three months and attaining sexual maturity at four months. This speed of maturation contrasts markedly with all Primates (Sprankel, 1960; Martin, 1966).

Reproduction

According to Butler (1964), it is generally agreed that reproductive organs are less likely to show structural changes dependent on differing environments than are most other organ systems.

In general, the genital organs of Tupaiidae are quite primitive for Eutheria. Strongest resemblances are with Metatheria on the one hand, and with higher Primates on the other. Insectivora, as well as Lemuroidea, appear to be somewhat deviant and specialized (Wood Jones, 1917; Eckstein, 1958).

Within Tupaiidae the genital system is somewhat less specialized in *Dendrogale* than in *Ptilocercus*, with both correspondingly different from the seemingly more advanced *Tupaia* (Davis, 1938).

Female Organs

An os clitoridis is present in the tip of the clitoris of *Tupaia javanica*. This may be a primitive mammalian feature since it is found in some insectivores (*Talpa*, *Erinaceus*) and in some prosimians (*Lemur*, *Cheirogaleus*, *Galago*) (Pehrson, 1914).

In *Tupaia glis* and *Tupaia ferruginea* the penis-like clitoris is elongate and pendulous (Hill, 1958a). Although the urethra of *Tupaia javanica* does not perforate the clitoris, Pehrson (1914) did observe a ventral groove throughout its length, continuous with the urogenital sinus. Lorisiform lemurs have the entire length of the clitoris tunnelled by the urethra (e.g., *Galago*). In lemuriform lemurs the urethral orifice lies at the root of the clitoris or may extend a short distance along its length (Butler, 1964). These variants indicate a rather primitive mammalian condition of urethral relations (Harms, 1956). In all living Primates the urethra and vagina open separately into the vestibule. The urethra and vagina of Tupaia join, as in many other primitive Eutheria (Martin, 1966).

Small litters (one to two individuals) are the rule among Primates (Petter-Rousseaux, 1964). Reduction in litter size may well be an adaptation to arboreal life. For tupaias, the long inter-suckling intervals would also probably limit litter size (Martin, 1966). The range is from one to four individuals per litter (Lyon, 1913; Wood Jones, 1917; Hendrickson, 1954; Sprankel, 1959). There has evidently been no immediate effect on anatomy of reproductive organs, except possibly to reduce the number of mammary glands (Lyon, 1913; Wood Jones, 1917; Carlsson, 1922). Insectivores tend to have larger-sized litters, with a recorded range from two (Macroscelididae) to twenty (Tenrecidae) (Asdell, 1964).

The reduction in number of mammary glands (one to three pairs), if related to the long inter-suckling periods in Tupaia, might well be a parallelism with the reduction in Primates, in which there is protracted gestation and postnatal care (Lyon, 1913; Wood Jones, 1917; Carlsson, 1922; Harms, 1956;

Asdell, 1964; Butler, 1964; Martin, 1966).

Elephantulus (Macroscelididae) demonstrates a type of uterine bleeding that may represent a functional parallelism with primate menstruation (Harms, 1956; Asdell, 1964).

There is no correlation between the presence of coiled arterioles in the uterine wall and menstruation. The distribution of the coiled arterioles in tupaiids differs from that in Old World primates (including humans and prosimians) in that these arterioles do not penetrate into the "functional zone" of the tupaiid endometrium (Luckett, 1967).

Luckett (1967) cites some evidence that captive tree shrews show slight loss of endometrial pad tissue following pseudopregnancy. This may be comparable to the slight menstrual bleeding observed in New World monkeys. Pseudopregnant cycles are probably rare among wild tree shrews. Little is known in general, however, about possible microscopic menses in Insectivora, Prosimii, or other mammalian orders.

Male Organs

The main features of the male ducts and accessory glands in tree shrews are of generalized primate form (Garrod, 1879; Engle, 1926; Le Gros Clark, 1926a; Eckstein, 1958; Butler, 1964). Although reproductive organs are reputed to be conservative, phylogenetic patterns are very difficult to follow in the references cited above. This may be due to preservation of series of mutations resulting from lack of any marked selection pressure. Any adaptive trends of long duration would probably yield patterns easier to interpret. Histochemical and histogenetic studies are needed to resolve numerous phylogenetic problems (Price, 1963; Butler, 1964).

In *Tupaia* the testes have permanently descended into a hairy scrotum. In *Ptilocercus*, however, descent is intermittent (seasonal), suggesting a restricted breeding season (Le Gros Clark, 1926a; Eckstein, 1958). Garrod (1879) observed that in a male specimen of *Tupaia belangeri* the large cauda epididymis alone descended into the rudimentary scrotum; the testes did not.

The patent but narrowed processus vaginalis of *Tupaia* also occurs in lower Primates, including most monkeys (Eckstein, 1958).

Most Insectivora show permanent retention of the testes intra-abdominally, with no true scrotum present. Testes in *Talpa* are intra-abdominal generally, although descending into small peritoneal pouches during the breeding season (Eckstein, 1958; Asdell, 1964).

Gregory (1910) remarked that Tupaiidae stand higher than "any other Insectivores" in permanent descent of the testes into a hairy scrotum, as opposed to temporary descent into a "cremaster sack"; yet he found Tupaiidae more primitive than typical eutherians in the following features: (1) the two testes are not appressed, each being enclosed within a separate cremaster sack in the scrotum; (2) the testes fail to descend beyond the penis, remaining anterior to it, as in Macropus (Marsupialia).

There is permanent descent of the testes in practically all Primates; exceptions include marmosets and some lemurs (Eckstein, 1958).

In Tupaiidae the position of the testes after descent into the scrotum is rather unique among eutherian mammals, suggestive of an intermediate phase between Metatheria and Eutheria (Wood Jones, 1917). Carlsson (1922) noted this position even in Tupaia embryos. Since the testes lie both cephalic and lateral to the body of the penis, the position is described by some as parapenial (Kaudern, 1910; Le Gros Clark, 1926a). Although usually described as prepenial, the position has also been likened to the mons veneris area of the female. In Metatheria the scrotal sacs lie cephalic to the site of the mons veneris area. In Eutheria, as a rule, the testes lie caudal to the mons veneris area (Hill, 1958a), except in Lagomorpha (Martin, 1966).

Among Insectivora, including Macroscelididae, the testes lie in a post-penial position (Gregory, 1910).

Although most Primates show the post-penial position, marmosets and certain lemurs display a parapenial position of the scrotal sac. Scrotal sacs may be parapenial or even prepenial in some species of gibbon. It is probable that this seemingly primitive condition must be a secondary adaptation in the gibbon species (Eckstein, 1958). This may also be true in tupaiids and lagomorphs (Martin, 1966).

The penis of Tupaiidae is semi-pendulous (Wood Jones, 1917; Eckstein, 1958). Hill (1958a) observed that the primate penis is invariably pendulous in some degree. Primates thus differ from the majority of mammals, with the exception of bats and bears.

The penis of _Tupaia_ is somewhat bent in a caudal direction. In Insectivora (disregarding _Chrysochloris_), the penis shows sigmoid flexure. Similarity to insectivores is no greater in the embryo, according to Carlsson (1922).

An os penis (baculum) is found in some insectivores, most primates, and many other scattered groups of placental mammals (Eckstein, 1958; Hill, 1958a); thus it may be a primitive eutherian feature. Its absence in Tupaiidae and numerous other mammals would then be due to secondary loss.

Gestation Period

Gestation periods are long in lemurs, compared with other mammals of similar size. Tupaiidae appear to be intermediate between Insectivora and Primates, showing a trend toward prolongation (forty-five to sixty days) (Snedegar, 1949; Hendrickson, 1954; Sprankel, 1959; Asdell, 1964).

Embryogenesis

It is difficult to evaluate, at this time, the phylogenetic significance of early embryogenesis in Tupaiidae. There are several seemingly unusual features. Only one species, *Tupaia javanica*, has been investigated. Little information is available on most Insectivora on the one hand, and many Prosimii on the other (Starck, 1956).

Extra-embryonic Membranes and Placentation

Extra-embryonic membranes and placentae in eutherian mammals must ultimately derive from membranes of the reptilian (cleidoic) egg; thus one would expect a primitive eutherian mammal to display: (1) a large yolk sac, (2) a choriovitelline placenta or homologue,

(3) a large allantois, (4) amnion formation by folding (Butler, 1964).

Hill (1965) believed that the basic mammalian stock from which Primates diverged must have had an arrangement similar to that observed in modern monotremes and marsupials:

> The outer wall of the embryonal formation consisted, over the lower hemisphere or thereabouts, of omphalopleure, vascularized in part or throughout by the vitelline or yolk-sac vessels, and over the remainder, vascularized by the umbilical vessels of the allantois. The vestigial shell membrane and the zona having already disappeared during the earlier stages of development, the primitive placenta was simply constituted by the close apposition of these two regions with the vascular lining of the uterus, and so was partly allanto-chorionic, partly omphalopleural in nature. Here, then, we have the simplest possible type of appositional placenta, the trophoblast being as yet a single layer, functional in absorption and gas exchange, but exhibiting no proliferative or invasive properties (Hill, 1965).

The occurrence of a diffuse epitheliochorial, non-deciduate placenta in groups as different as Lemuroidea, Pholidota, Artiodactyla, Perissodactyla, Proboscidea, Cetacea, and Sirenia could be interpreted as due to persistence of an ancestral condition (Grosser, 1933; Hill, 1965).

Among Insectivora an epitheliochorial placenta occurs in <u>Scalopus aquaticus</u> (Talpidae) (Mossman, 1939). Epitheliochorial paraplacental arrangements are found in Centetidae, Potamogalidae, and Macroscelididae (Starck, 1956).

Since an embryo gains access to a uterus with an intact epithelium, there must be an initial epitheliochorial connection. Yet, probably already in Promammalia, several placental arrangements appeared. Reptiles show epitheliochorial, syndesmochorial, and endotheliochorial types of placentae, including a major portion of one type and associated accessory structures of another type (Starck, 1956). Similar combinations are found in Insectivora, in which the hemoendothelial type may also occur. Echinosorex, one of the most generalized of the lower Erinaceidae, shows a hemoendothelial, discoidal chorioallantoic placenta, with a choriovitelline placenta lying peripheral to it (Meister and Davis, 1953).

Since the hemochorial type of placenta occurs in some insectivores, Hubrecht (1899) and Wislocki (1929) regarded this invasive type as primitive for eutherian mammals. On this view, the non-invasive epitheliochorial type (as in lemurs) would exemplify specialized reduction.

Tupaia species possess an endotheliochorial placenta, according to van der Horst (1949), Hill (1965), and Luckett (1967). Other workers (Hubrecht, 1899; de Lange, 1933; Mossman, 1937; Strauss, 1942; Meister and Davis, 1956) have classified it as hemochorial, at least near term. Since he supervised Luckett's (1967) work, Mossman's view has changed.

Also in dispute is the presence and degree of development of a choriovitelline placenta at an early stage of gestation. Although Meister and Davis (1958) found no evidence of a yolk-sac placenta at any stage in Tupaia tana, Starck (1956), Hill (1965), and Luckett (1967) have found well-formed, functional choriovitelline placentae in several species of Tupaia, Lyonogale, Urogale, and Dendrogale. The yolk-sac placenta persists to the early limb-bud stage.

Features of the tupaiid placenta and fetal membranes that are regarded as primitive are listed below:

1. The depth of implantation is superficial; there is no decidua capsularis (Mossman, 1937).
2. In Tupaia minor, Meister and Davis (1956) found the uterine epithelium to remain intact beyond the placental margin. Over the entire decidua parietalis, chorionic epithelium is in contact with the uterine epithelium.
3. Hill (1965) stated that "the occurrence of functionally active glands in the endometrium of the pregnant uterus is a feature which links the placenta of Tupaia with those of the epithelio-chorial type." Luckett (1967) found these glands active in secretion

throughout pregnancy.

4. In *Tupaia* no fetal or maternal giant cells appear at any stage of development (Hill, 1965).

5. At parturition, in *Tupaia*, the placenta is not expelled as an after-birth, according to Starck (1956). Rather, as in *Talpa*, it is locally resorbed ("contra-deciduate" type). Luckett (1967), however, refutes this view.

6. Amniogenesis is by folding (cavitation to form a primitive cavity, followed by folding) (Mossman, 1937). This also occurs in *Talpa* (Insectivora) and in *Galago senegalensis* (Prosimii) (Starck, 1956; Butler, 1964).

7. The yolk sac is well developed and completely vascularized. There is evidently a true yolk-sac placenta for a time.

Among mammals a large, free, vascular yolk sac is characteristic of Carnivora, Tupaiidae, and Strepsirhini (e.g., *Galago senegalensis*) (Starck, 1956; Butler, 1964; Luckett, 1967). Centetidae (Insectivora) and most Primates have a reduced or vestigial, free, vascular yolk sac. Most Insectivora have inverted yolk sacs (Luckett, 1967).

Starck (1956), Meister and Davis (1958), and Hill (1965), regarded the tupaiid yolk sac as waning since omphalopleural mesenchyme shows little or no tendency to penetrate the "villi," whereas allantochorionic mesenchyme does.

8. Refuting Meister and Davis (1958), Luckett (1967) found the allantois of tupaiid species to be a large, flattened vesicle persisting in the late stages of pregnancy. It fuses with the chorion to cover most of the surface of the placental discs.

A large, lobed allantois has been observed in _Galago senegalensis_ (Strepsirhini) (Butler, 1964).

9. Trophoblastic villi are rather poorly developed. Hill (1965) found them to be variable in size and shape in _Tupaia dorsalis_.

10. In _Dendrogale_, Luckett (1967) observed small depressions in the smooth chorio-allantoic membrane. He believed these to be homologous to the paraplacental absorptive areas found in all groups with an epitheliochorial placenta, as well as in Carnivora, Talpidae, and Tubulidentata.

Luckett (1967) found the development of tupaiid fetal membranes to be most similar to that in Carnivora, Talpidae, and Soricidae (in the order given). Common to these groups are an endotheliochorial placenta and retention of both a large allantoic vesicle and yolk sac. It is the morphogenetic relationships of the most conservative features of fetal membranes that are of phylogenetic significance and not simply their appearance in late stages of pregnancy. Since these are primitive features, the resemblance is believed to be due to conservatism.

Mossman (1937) believed that the earliest placentation in mammals was diffuse epitheliochorial in type. Correlation of evidence from the fossil record with that of the morphogenesis of fetal membranes has recently led Mossman to postulate a dichotomy of fetal membrane characteristics in the primitive eutherian stock (late Cretaceous to early Paleocene) (Luckett, 1967). The ancestral insectivore-like stock giving rise to all taxa with a deciduate placenta presumably had a broad zonary, labyrinthine endotheliochorial placenta, with large allantoic vesicle and large, free, vascular yolk sac. Among living mammals this situation is found only in Carnivora and Tupaiidae. No problems of homology are posed by the double discoid placentae of tupaiids since carnivore placentae vary from complete zonary, through incomplete zonary, to double and single discoid types (Luckett, 1967). Repression of portions of the broad zone would lead to retention of localized disc(s).

It is further postulated by Mossman and Luckett (1967) that the order Condylarthra (basic ungulate stock) retained the more primitive, diffuse epitheliochorial placenta, with large allantois and yolk sac. Since there is no good fossil evidence that primitive lemuroids ever gave rise to anything but other lemuroids, having evolved separately since late Cretaceous or early Paleocene times, they may well have retained the primitive, diffuse epitheliochorial placenta of ancestral mammals. On this view, lemuroids and primates may show convergent evolution in other features for adaptation to an arboreal habitat.

Integumentary System

Evidence from histology of the tupaiid skin is indicative of probable primitive insectivore status. Montagna, Yun, Silver, and Quevedo (1962) demonstrated that, unlike that of primates, the tree shrew's skin is rather thin; the sebaceous gland cells contain small, rounded lipid droplets of rather uniform size; hair follicles are arranged in rows and show no glycogen and phosphorylase in the quiescent phase. Some of these features are shared with other primitive orders, such as bats and rodents. More information is needed concerning the gland types found in the hairy skin of Insectivora, Dermoptera, and Chiroptera before one can evaluate the significance of the presence of eccrine sweat glands in *Tupaia glis* and in Anthropoidea, despite their absence in Prosimii generally.

The phylogenetic significance of the volar integument has been discussed by Biegert (1961, 1963). In adaptation to an arboreal life, prosimians and tupaiids (no other modern insectivores being tree dwellers) have developed three-dimensional vision and touch. As expected, Tupaiidae approximate a primitive primate model showing distinct advances over all Insectivora. While volar pads appeared in very early mammals and friction skin appeared secondarily by convergence in several mammalian lines, all Recent primates are distinguished by the rather stable pattern of characteristic ridges. The configuration of the embryonic pad determines the ridge pattern thereby established for life. This pattern is shared with all primates, only by Tupaiidae. If due to parallelism, there seems to be some common genetic background. Elephant shrews (Macroscelididae, the second menotyphlous family) show a far more primitive condition resembling that of Reptilia. (In many other features Macroscelididae show greater specialization or divergence from the basic mammalian stock; thus it appears that Tupaiidae and Macroscelididae must have diverged from each other very early.)

A resemblance between <u>Tupaia</u> and <u>Lemur</u> lies in the pattern of flexion creases on palmar and plantar skin surfaces (Biegert, 1961).

In all primates, at least one pair of digits bears nails. As in all primitive and generalized mammals, tupaiids possess claws on all the digits. Although McKenna (1963) recently questioned the status of Anagale (lower Oligocene genus of eastern Asia) as a fossil tupaioid, it was long considered so (Simpson, 1931). Although the manus in Anagale has claws, "the terminal phalanges of the pes are flattened and spatulate distally rather closely approximating the distal phalanges of some primitive lemuroids" (Le Gros Clark, 1936).

The arrangement of hairs (in tufts associated with scales) on the tail of Ptilocercus, the pen-tailed tree shrew, is a very primitive mammalian characteristic (Gregory, 1910; Le Gros Clark, 1926a).

Among mammals, only most Marsupialia possess the full complement of facial vibrissae in typical arrangement (Pocock, 1914). The Tupaiidae retain a nearly complete and well-developed facial complement. Within many orders, including Insectivora and Primates, vibrissae show reduction, especially in the higher, derivative species (Pocock, 1914; Carlsson, 1922).

Endocrine System

Histologically, the eminentia mediana (of hypothalamus) in most mammals, including most non-hominoid primates, is a simple, two-layered structure. Tupaia glis shows incipient stages of the primate trend toward a breaking up of the external layer into "separate perivascular regions around the capillaries of the portal vessels in the interior of the eminentia" (Hanström, 1958).

Another feature shared by Tupaiidae and some Primates, but not by any of six genera of Insectivora examined, is a common caudal fold formed by pars distalis and pars intermedia (Hanström, 1958).

A feature of the tupaiid suprarenal glands indicative of the primitive mammalian condition (shared with Marsupialia and Insectivora, e.g.) is the variation in their position. Constancy of position is greater, even in lemurs, among primates (Le Gros Clark, 1926a; Bourne, 1936, 1949; Bachmann, 1958).

Although unusually broad for a primitive mammal, the adrenal cortex of Tupaia montana shows an indefinitely fasciculated arrangement of cells. (All mammals show some degree of fasciculation.) No zona reticularis has been noticed, although present in most mammals. In lack of definition of cortical zones, lemurs show little advance over tree shrews. Tarsiers and the higher primates show three clearly defined zones. In all Insectivora examined (three genera), the three zones typical of higher Primates and most Mammalia are present. It seems that the lack of differentiation in *Tupaia* species is a primitive feature; yet it may be secondary (Bourne, 1949; Bachmann, 1958).

Urinary System

In major features--smooth contour and unipapillate medulla--Tupaiidae resemble primitive Mammalia, such as Monotremata, Marsupialia, Insectivora, and Rodentia, as well as most Primates. The apex of the medulla is intra-ureteric, as in some lower mammals including Lorisiformes and Tarsiiformes among Primates (Straus and Arcadi, 1958).

Respiratory System

Although the elongated upper portion of the larynx projects into the nasopharynx in Insectivora, *Tupaia*, and many lower Primates, the structure of this vestibular region differs among them. In Insectivora (e.g., *Erinaceus*, the European hedgehog) the wall of this funnel-like projection is composed of the middle portion of the epiglottis and the aryepiglottic folds. In *Tupaia*, *Loris*, *Perodicticus* (potto), and *Galago*, however, the lateral epiglottic folds are well developed, with the smaller aryepiglottic folds lying in the inner wall (Starck and Schneider, 1960).

Digestive System

There is considerable indirect evidence that primitive placental mammals were small and semi-arboreal. The foods readily available to such animals would be eggs, nestlings, insects, and fruits. Such insectivorous-omnivorous habits would prevent over-specialization of any one part of the digestive tract. The tupaiid diet of insects and fruit may be considered a primitive marsupio-placental feature. Lipotyphlous insectivores early became specialized for a more exclusively insectivorous diet; primates, including lemurs, became more omnivorous or herbivorous (Sonntag, 1925; Wharton, 1950, Grassé, 1955).

Teeth

Tupaiid cheek teeth are rather typically insectivorous. In the arboreal Tupaiidae and Lemuroidea, the lower incisors are procumbent in some degree, and these animals use their hands to hold food while eating (Lyon, 1913; Buettner-Janusch and Andrew, 1962).

Palatine Ridges

Schultz (1958) stated that palatine ridges are found in practically all mammals, although number and size vary. The probable primitive condition persists in many marsupials and insectivores. The opossum, e.g., has seven to eight pairs of well-developed rugae. In Tupaia species, seven pairs of strongly developed, regularly arranged ridges are present (Garrod, 1879; Schultz, 1958). In Ptilocercus, Le Gros Clark (1926a) found nine transverse pairs, each corresponding to a tooth, from the second incisor backwards. Prosimians remain unspecialized, having seven to eight pairs of well-developed rugae with regular symmetry (Le Gros Clark, 1926a; Schultz, 1949).

Tongue

Sonntag (1921, 1925) hypothesized that the primitive mammalian tongue had two major components; lingua and sublingua, each with considerable independence of movement. The sublingua may be the morphological equivalent of the infra-mammalian tongue. With increased development of muscles and papillae in and near the dorsum, a mammalian tongue would have emerged. The os entoglossum (cylindrical axial rod near lower surface) and the remainder of the lower part of the tongue would then become the lytta (lyssa) and the sublingua, respectively. With subsequent adaptive radiation of primitive mammalian orders, certain (inferior) parts tended to disappear by absorption into the septum linguae and under surface of the tongue. Only Menotyphla and Primates retained both lytta and sublingua, in some members. In Tupaia and Lemuroidea there is far less reduction--perhaps even secondary specialization--of the sublingua, as compared with Macroscelididae and Tarsius. In its greater length and muscular development, the tupaiid lytta remains better developed than in prosimians (Sonntag, 1921; Le Gros Clark, 1926a; Machida, Perkins, and Giacometti, 1967). Since lytta and sublingua are derived from the reptilian tongue, they can scarcely be interpreted as new acquisitions appearing independently in Prosimii and Menotyphla; thus Sonntag (1921) concluded that we must assume a common origin for both groups from Mesozoic Menotyphla, a group designated by Gregory (1910) as "insectivorous pre-Primates."

Marsupialia retained only the sublingua; Lipotyphla, only the lytta. Groups having lost both portions of the tongue include Chiroptera, Dermoptera, and Monotremata (Sonntag, 1925).

Like the primitive mammalian tongue, that of tupaiids is long and slender, tapering somewhat toward the rounded tip. Indicative of the primate trend is a concentration of fungiform papillae on the tip. As in Marsupialia, most Insectivora, and smaller Primates generally, there is a triad of vallate papillae (Sonntag, 1921).

Gall Bladder

Carlsson (1922) found the prominent gall bladder of *Tupaia* species lying in the cystic fissure, on the diaphragmatic surface of the liver, at the right margin of the central lobe. This resembles prosimians (especially *Galago* and *Lemur*) and differs from Insectivora. In *Erinaceus*, for example, the gall bladder lies in the middle of the central lobe. However, some variation exists within Tupaiidae. Le Gros Clark (1926a) pointed out that *Ptilocercus* has the gall bladder situated in the middle of the right central lobe, as in lipotyphlous Insectivora. This is regarded as the more primitive relationship. In the position of the gall bladder, *Dendrogale* (smooth-tailed tree shrew) resembles *Tupaia* (Davis, 1938).

Small Intestine

According to Hill (1958b), the small intestine is primitively of the same calibre throughout its length. This condition persists in *Tupaia* and *Tarsius*.

In primitive mammals the entire length of the small intestine is freely suspended by a median dorsal mesentery from the abdominal wall. Such a simple series of mobile coils, arranged without discernible order, is found in tree shrews (*Dendrogale* and *Ptilocercus*), some lemurs, *Tarsius*, and an occasional platyrrhine monkey (e.g., *Saimiri*, the squirrel monkey) (Le Gros Clark, 1926a, 1959; Davis, 1938).

The phylogenetic stages in development of the duodeno-jejunal flexure and consequent gut rotation are recounted by Hill (1958b). The sharp bend at the duodeno-jejunal junction occurs in all Primates, as well as Tupaiidae, and is caused by fixation of the gut to the dorsal body wall at this point. This duodeno-jejunal flexure becomes the pivot of clockwise rotation of the lower gut. *Ptilocercus* shows minimal rotation: the colon remains on the left (Le Gros Clark, 1926a); migration in *Dendrogale* is similar (Davis, 1938). *Tupaia* and *Tarsius* (with some individuals showing more advance than others) show lengthening of the large intestine, with the ileocolic junction swinging dextrad around the periphery of the coiled jejuno-ileum. Within the right flank the caecum points dextro-craniad in *Tupaia*; in *Tarsius*, where longer, caudad. Lemurs, lorises, and most simians show more advanced ileo-colic migration. (Note, however, that certain lower mammals show the greatest ileo-colic migration. An example is *Vombatus*, a marsupial.)

Large Intestine

The primitive mammalian large intestine is believed to be a short, straight, simple tube of relatively wide diameter and not clearly differentiated into colon and rectum. It proceeds directly caudad, to the anal canal. It is suspended in the midline by a continuous dorsal mesentery. In retaining this pattern, *Ptilocercus* was regarded by Le Gros Clark (1926a) as "almost reptilian." Hill (1958b) also found a young specimen of *Tupaia tana tana* to be almost reptilian in hind-gut features. As in iguana, e.g., he noted the especially capacious cranial end, with ileum entering on the right anterior aspect, and with the caecum being a slight bulge in the antero-sinistral wall. Davis (1938) noted that in *Dendrogale* the colon is even less differentiated than in *Ptilocercus*, for its diameter was found to be no greater than that of the small intestine; *Saimiri* and *Tarsius* are somewhat similar (Starck, 1958; Le Gros Clark, 1959).

Chapman (1904) found the large intestine of *Tupaia ferruginea* and *Tupaia pictum* to be of uniform diameter throughout. In *Tupaia*, as in *Loris*, *Saimiri*, and *Callicebus*, taeniae and haustra are lacking; the colon cannot readily be distinguished from the rectum. One, two, or three taeniae first appear in certain lemur species (Hill, 1958b).

Le Gros Clark (1926a) detected no differentiation within the colon of *Ptilocercus*, except by observing the blood supply. In *Tupaia*, however, the upper end of the colon bends dextrad to give the appearance of an incipient demarcation between a transverse and descending colon. *Tarsius* shows a further step in having a quite well-defined transverse colon (Le Gros Clark, 1959).

A slightly more advanced differentiation may be seen in *Tupaia (Anathana) elliot*i and *Tupaia tana*. Here, Hill (1958b) found the ileocolic junction in the right mid-flank area. Thus, a short ascending colon runs craniad, toward the liver, and then arches over the duodenum as a complete transverse colon.

Mesenteric Relations

Tree shrews show the primitive mammalian arrangement, with even the duodenum suspended freely by the dorsal mesentery. This condition of intestinal motility from stomach to rectum persists in some lemurs, in *Tarsius*, and in a few platyrrhine monkey species, such as *Saimiri*. All Insectivora also show continuity of the dorsal mesentery (Hill, 1958b).

Starck (1958) observed that all Primates and Tupaiidae possess a mesotyphlon (a peritoneal fold between caecum and ileum). In primitive mammals this fold is non-vascular and devoid of fat. Vessels, when present, enter via adjacent vascular plicae.

Basically, the vascular folds are symmetrical and short, lying to right and left of the true non-vascular mesotyphlon. Although most Callithricidae (marmosets and tamarins) retain this symmetry, *Tupaia*, like most Primates, shows enlargement of the left (dorsal) vessels. The ventral caecal artery remains small.

Sensory Structures

Cutaneous Receptors

Winkelmann (1963) observed that in *Urogale everetti* there were no papillary nerve endings of the Meissner or mucocutaneous type, such as are found in all Primates, including Lemuroidea. More difficult to explain phylogenetically is the presence of such specialized endings in only one other mammalian group, namely, *Didelphis virginiana* (Marsupialia) (Winkelmann, 1964). Until studies have been made of other marsupial and insectivore species, no interpretation seems in order. Also of interest is Winkelmann's (1963) failure to find any typical mammalian end organs in *Urogale*; although he believed further study would reveal them.

Tupaiidae retain the primitive mammalian type of rhinarium: the external nares are surrounded by an area of naked, moist glandular skin (Hill, 1953b).

Olfactory Receptors

Being primarily ground-dwellers, most primitive mammals (including insectivores) have a keen olfactory sense (Polyak, 1957; Negus, 1958). Since tree shrews are in some measure arboreal, it is notable that vision has increased concomitant with suppression of olfaction. Least apparent in tree shrews, this suppression increases as the primate scale is ascended, through lemurs and monkeys, to higher apes and man (Negus, 1958).

The cartilages associated with the vomeronasal organ (of Jacobson) are discussed with the skull.

Ears

As in most lower Primates and mammals generally, the pinna is more or less freely movable. Lasinski (1960) maintained that the primitive form of the primate ear was of a rounded or oval shape, as in *Tupaia*. This general form is also found in Primates that are diurnal. Even the incurling of the peripheral margin corresponds to the helix found in monkeys, apes, and man. Other landmarks, such as tragus, antitragus, antihelix, and crura, also resemble those of higher Primates.

Bony features of the ear region are discussed with the skull.

Eyes and Accessory Structures

The tree shrew has larger eyes than other shrews. This is usually considered to be a primate-like feature (Polyak, 1957).

The well-developed Harderian gland and the fair (covering one-third of corneal surface) development of the nictitating membrane, in tupaias, are generally found among primitive mammals (Le Gros Clark, 1926a).

Tupaia has monocular vision, primarily. As in all infra-mammalian vertebrates and many mammals, there are few or no uncrossed nerve fibers in the optic chiasma (Polyak, 1957; Campbell, Jane, and Yashon, 1967).

In mammals generally, the cornea is thicker than the sclera. The most extreme difference known is found in *Callithrix jacchus*, with a corneal diameter of 256-360 micra, and only 56 micra for the sclera. This is five to six times as great as the difference previously found to be unique among mammals. *Tupaia*, however, shows similar values: the cornea is 200 micra in diameter; the sclera, only 35 micra. Similar relations, although not as extreme, are found in *Perodicticus*, *Galago*, and *Nycticebus* (Rohen, 1962).

Most Primates lack a Bowman's membrane; *Tupaia glis* and Hominoidea, however, have such a cell-free, homogeneous-appearing layer beneath the basement membrane of the corneal epithelium (Rohen, 1962).

Samorajski, Ordy, and Keefe (1966) have made a careful study of the retina of *Tupaia glis*, using fundus photography, histochemistry, and electron microscopy. Polyak (1957), Le Gros Clark (1959), and Rohen (1962) had indicated the presence of incipient "central area" formation in *Tupaia* and *Urogale*, based on the diminished number of finer retinal vessels observed here, in contrast with more peripheral retinal regions. Samorajski, Ordy, and Keefe (1966), however, have found the branches of the prominent central retinal artery to radiate uniformly over the retinal surface. The single layer of short, thick cones extends uniformly across the central and peripheral zones of the retina. Cells of the ganglion layer extend in a double row across the retina, with no thinning so characteristic of the fovea of higher Primates. (No comparable studies have yet been done on Prosimii.)

The high visual acuity of higher Primates and man is matched by *Tupaia*, as indicated by behavioral study (Ordy and Keefe, 1965). In the absence of a fovea centralis, it has been suggested that in this tree shrew the entire retina may function as a crude sort of central area (Samorajski, Ordy, and Keefe, 1966). This would indicate a kind of evolutionary parallelism at the functional level.

Certain ultrastructural features (e.g., the nature of saccules in the cone outer segments) are shared by Tupaia with monkeys, apes, and man, in contrast with any other lower animals studied. On the other hand, a unique feature (observed in no other animals) is the highly ordered, whorled lamellar configuration of concentrated cristae found in the mitochondria of the cone inner segments. Without comparable observations on other diurnal insectivores and prosimians, it is difficult to evaluate these findings of Samorajski, Ordy, and Keefe (1966).

In Urogale everetti there is a long, thin cone-shaped formation (almost entirely of neuroglia) with its base on the optic papilla and pointing into the vitreal cavity. A similar structure is found in lizards (Polyak, 1957).

Insectivora generally show some degree of microphthalmia and poor sight. Vision shows close correlation with mode of life among mammals generally. This poses a problem regarding vision in relation to mammalian origins, as discussed by Polyak (1957). Insectivora are acknowledged as the most primitive of living Eutheria. The earliest mammalian fossils are insectivorous; thus, if early mammals derived from large-eyed, keen-sighted reptiles, Insectivora must have undergone secondary reduction due to their way of life. On the other hand, if the earliest mammals or mammal-like reptiles underwent reduction of vision, an "evolutionary bottleneck" would have resulted, with marked reorganization of the sensory faculties. Whereas certain insectivores and bats showed reduction or loss of vision, perhaps certain tropical shrews, becoming arboreal, would have acquired a dominant visual sense.

The modern tree-shrew eye can scarcely be considered generalized mammalian in type, being almost exclusively specialized for photopic vision; thus Polyak (1957) believed that tree shrews illustrate the stage just preceding the coming of true Primates, only in a general way.

Parallelism or not, as in unquestioned Primates, there must have been considerable eye-brain reciprocity in the phylogenetic development of modern tree shrews. -- Polyak (1957) called them "born busybodies," for they are constantly examining everything around them, even when not hungry. -- The nervous system shows much evidence of such concomitant development.

Nervous System

Brain in General

In brain weight relative to total body weight, tree shrews are comparable to elephant shrews on the one hand, and to lemurs of comparable size (e.g., *Microcebus*) on the other (Le Gros Clark, 1928, 1959; Evans, 1942; Campbell, 1966). More data, based on a larger variety of mammalian groups, are needed before this characteristic can be evaluated from a phylogenetic point of view.

Telencephalon

In contrast with *Macroscelides* and *Centetes*, the cerebral hemispheres of tree shrews extend back over the anterior cerebellum, leaving no part of the diencephalon or midbrain visible in a dorsal view. This is similar to the situation in lemurs (Le Gros Clark, 1959).

In relation to body weight, Stephan and Andy (1964) found that the telencephalon (of the five secondary brain vesicles) shows the greatest phylogenetic development. In monkeys, it is six and one-half to seven and one-half times the size found in basal insectivores (*Tenrec*, *Setifer*, *Erinaceus*, *Crocidura*, *Sorex* species). Following in descending order are prosimians, *Tupaia*, Macroscelididae and *Galemys*, trailed by other insectivores.

In relation to body weight the neocortex of monkeys undergoes tremendous growth, reduced by half in prosimians. *Tupaia* has a neocortical size between the lower primates and the highest insectivores (*Galemys* and Macroscelididae). The other insectivores show little neocortical development in relation to the basal forms; smallest of the latter are *Tenrec* and *Setifer* (Stephan and Andy, 1964).

The corpus striatum shows the next greatest development (among telencephalic subdivisions). It is largest in monkeys, somewhat less developed in prosimians, approximately equal for *Tupaia* and *Galemys*, with all other insectivores following (Stephan and Andy, 1964).

The hippocampus is larger in specialized insectivores (e.g., Macroscelididae) than in monkeys and some prosimians; yet in *Tupaia* and *Loris* its size is close to that of basal insectivores (Stephan and Andy, 1964).

Andy and Stephan (1966) pointed out that the true septum *appears* to decrease in size when compared with corpus callosum or with total brain volume, as one progresses from primitive insectivores through tupaiids and prosimians to higher primates and man. However, in comparison relative to body size, using a regression line based on primitive insectivores, the septum is observed to undergo a definite increase in size, phylogenetically.

Expansion of the neopallium in tupaiids (beyond most insectivores) appears to be primarily in a posterior direction, due to an enlarged visual cortex. This has tended to displace both the rhinal sulcus and the temporal cortex downwards. While it is true (Le Gros Clark, 1959) that the position of the rhinal sulcus is more comparable to *Microcebus* than to *Centetes* or *Echinosorex*, there is equivalent or almost-equivalent downward displacement in a variety of other mammals: *Trichosurus*, *Dasyurus*, *Petrogale*, *Onychogalea*, *Aepyprymnus* (order Marsupialia); *Myocastor*, *Cavia*, *Dasyprocta*, *Tamias*, *Sciurus* (order Rodentia); *Oryctolagus* (order Lagomorpha) (Campbell, 1966).

While neocortical expansion in *Tupaia* does involve chiefly the occipital cortex, the temporal cortex shows some expansion, too. A distinct temporal pole is formed. The frontal lobe, however, remains small. Frontal and parietal association areas are not elaborated. Such areas first become recognizable in lemurs, and are especially characteristic of Anthropoidea (Le Gros Clark, 1959).

Overall, the neocortex of tree shrews shows increased cellularity and better differentiation of laminae than in insectivores, although poorer than in most lemurs. The various cortical areas can be distinguished by cytoarchitectural features (Le Gros Clark, 1959).

In Insectivora increase in size of the brain as a whole involves enlargement of the pyriform lobe disproportionate to that of the neocortex (e.g., *Echinosorex*). In *Tupaia*, as in Primates generally, neopallial expansion accompanies relative regression of the pyriform lobe (Le Gros Clark, 1959).

Except for the calcarine (limiting) sulcus of the visual cortex, there is little indication of neocortical convolution in tupaiids. Le Gros Clark (1924a) noted intercalary and presylvian sulci, as well as some other incipient sulci (subzonal foldings) in *Tupaia*. A lateral (Sylvian) fissure is not observed below lemurs; a central sulcus, although occurring sporadically among lemurs, is not a constant feature until one reaches anthropoid levels above marmosets.

The corpus callosum of *Tupaia* is thin and nearly straight. Although *Microcebus* adds anterior (genu) and posterior (splenium) thickenings, the insectivores and tarsioids show poorer development than *Tupaia*. A notable exception is found in *Macroscelides* (Elliot Smith, 1902). Here the corpus callosum shows quite extraordinary development for an insectivore. Although it is large, with definite splenium, it is peculiar in being high up near the dorsal margin of the hemisphere, as well as in having a long, hook-like genu ending in a sharp rostrum. This would appear to be a case of rather specialized parallelism with lemurs and other primates.

Von Bonin and Bailey (1961), in discussing patterns of the cerebral cortex, noted that although the neocortex of Insectivora is much clearer than in reptiles (where it first appeared), the cellular layers and subdivisions into fields are difficult to relate to those of higher mammals. Like Brodman (whose work of 1909 they cite), they found the subdivisions to be vague. Only the insular cortex is definitely distinguishable. (Archipallium still constitutes over three-fourths of the cortex in insectivores.) *Elephantulus* was found to resemble *Erinaceus* in these respects. Von Bonin and Bailey (1961) further stated: "The brain of *Elephantulus* is clearly that of an Insectivore while that of *Tupaia*, in marked contrast, has the unmistakable primate pattern."

Like Brodman, von Bonin and Bailey (1961) found the motor area of *Tupaia* clearly recognizable; giant pyramidal cells in area four are very clear.

There is, in *Tupaia*, a temporal area which may have to do with hearing. There are other recognizable areas: parietal, insular, and frontal on the lateral aspect; retrosplenial (small) and limbic areas (over the anterior two-thirds of corpus callosum) on the medial aspect (von Bonin and Bailey, 1961).

Von Bonin and Bailey (1961) believed that the cortex of *Elephantulus* shows aberrant features in areas and their histology. As is generally true of insectivores and rodents (but not of higher forms), the retrosplenial areas are large in *Elephantulus*. The thickness of cortical layers I and IV are not at all in the same range as for Primates, including tree shrews.

The prominence of the occipital pole in *Tupaia* contrasts with *Macroscelides* and Lipotyphla. In *Tupaia* the occipital pole overlaps the corpora quadrigemina; however, this also occurs in numerous other mammals (Campbell, 1966). Histologically, the striate area is quite large and covers the dorso-occipital pole of the cerebral hemisphere, extending forward to the calcarine sulcus on the medial aspect. In *Tupaia* the calcarine sulcus is a *limiting* sulcus, not an *axial* sulcus of the striate area; thus the presence of a calcarine sulcus may be questioned as indicative of affinity with higher Primates. Further, a calcarine sulcus is absent in the presumably more primitive Ptilocercus. The phalanger, Trichosurus, has a much more prominent and extensive calcarine sulcus; in a marsupial, this trait would appear to be clearly due to convergence.

Tupaiidae show no retrocalcarine sulcus, found in primitive lemurs (e.g., Microcebus) and all higher Primates (Le Gros Clark, 1959).

The striate area of tupaiids shows greater cellularity and better differentiation of laminae than in any insectivores. Although interpretation of the cell layers is controversial, there is some evidence of an incipient "white line" of Gennari, as found in Primates generally. This is evidently effected by duplication of the inner granular layer, which is very conspicuous and sharply defined. Von Bonin and Bailey (1961) confirmed Le Gros Clark's view (1924a) that the striate area does begin to show the primate pattern in which layer IV is duplicated. They found the striate area of Insectivora to have none of the features observed in Primates. On the other hand, Campbell (1966) did not believe Le Gros Clark (1924a, 1925) demonstrated any detailed similarity between lamina IV of Tupaia and that of any primate. Although the presence of well-defined laminae in the tupaiid striate cortex is unquestioned, it is not yet possible to say whether this similarity to Primates is due to lineal ancestry or to parallelism.

The olfactory bulb of Tupaia remains rather large, compared with primates generally; compared with most terrestrial insectivores, it is somewhat reduced. Elephant shrews (with jumping habits), show a comparable reduction in the olfactory areas of the brain. Arboreal squirrels show even greater reduction than tree shrews and elephant shrews (Le Gros Clark, 1959).

In tupaiids the temporal pole is still formed by the pyriform lobe, as in some lower primates (lemuroids and tarsioids) (Le Gros Clark, 1959).

The tuberculum olfactorium of Tupaia is only slightly raised from the forebrain surface, in contrast with its prominent rounded shape in most small macrosmatic mammals of similar size (Le Gros Clark, 1959).

In Macroscelides there is a psalterium of crescentic shape, found elsewhere only in Metatheria. The hippocampal formation extends forward onto the upper surface of this (anterior) commissure, as in the Metatheria. In Tupaia the psalterium ends anteriorly in a slight bulbous swelling. A similar configuration is found in Microcebus. The hippocampal complex is reduced in Tupaia, relative to Insectivora (Le Gros Clark, 1959).

Diencephalon

In contrast with insectivores, there is an increased degree of differentiation of the thalamic nuclei in Tupaia (Le Gros Clark, 1929). Lamination of the lateral geniculate nucleus, although present, is not sharply defined (Woollard, 1926). Seemingly progressive features shared by tupaiids with primates include: (1) well-developed dorsal and ventral portions of the lateral geniculate nuclei, with rudimentary lamination in the dorsal portion; (2) enlargement of the pars posterior of lateral nucleus; (3) prominence of the pretectal nucleus (Le Gros Clark, 1932). The first two features are also found, however, in Trichosurus vulpecula, with dorsolateral geniculate nuclei even better differentiated than in Tupaia. The shape of the laminae in the phalanger approaches that of lemurs, in which optic tract fibers enter along the lateral convexity and optic radiation fibers leave the medial concave aspect (inverted type of lateral geniculate body--as opposed to everted type in Anthropoidea). In the phalanger, crossed (75 per cent) retinal fibers end chiefly in laminae one and three; uncrossed (25 per cent), chiefly in laminae two and four. Laminae one and two do show some overlap.

Higher Primates show a much more complete segregation of crossed from uncrossed fibers (Goldby, 1941).

Packer (1941) suggested that the degree of lamination is probably related to the degree of development of binocular vision in an animal.

Having studied sections of the visual cortex, Packer (1941) doubted if this area in the phalanger differs significantly from other primitive mammals. While lamina IV has fewer cells along its outer border, there is no suggestion of a subdivision within this layer (well marked in Tarsioidea and Anthropoidea, less clearly defined in _Tupaia_ and Lemuroidea).

Bauchot (1959) made a cytoarchitectural study of the diencephalon of _Talpa europaea_ (mole), generally quite similar to that of Marsupialia, Rodentia, and Chiroptera. The lateral geniculate body is rather reduced, as in most Insectivora, except _Macroscelides_ and _Tupaia_. It lacks the lamination found in _Tupaia_.

Campbell, Jane, and Yashon (1967) made a comparative study of retinal projections in tree shrew and hedgehog. The visually advanced _Tupaia glis_ showed a tendency toward restriction of mesencephalic and diencephalic terminations.

Glickstein, Calvin, and Doty (1966) compared the laminar structure of the dorsal geniculate body of *Saimiri* and *Tupaia* by degeneration experiments. *Saimiri* (squirrel monkey) shows a six-layered structure similar to that of Old World Primates. Layers one, four, and six show transneuronal degeneration contralateral to the enucleation; layers two, three, and five show degeneration ipsilaterally. *Tupaia*, with five layers in the nucleus, shows transneuronal degeneration of the (few) uncrossed fibers in layers one and five. The decussating fibers (overwhelming majority) connect with internal layers two and four of the nucleus. Layer three did not seem to be differentially degenerated on the crossed and uncrossed sides.

According to Campbell (1966), every primate examined shows a pattern resembling *Saimiri* (reverse of *Tupaia*), with crossed fibers terminating in the innermost and outermost lamellae. This suggests that the lamination observed in the dorsal lateral geniculate nucleus of tree shrews is the result of convergent or parallel evolution.

Schroeder, Yashon, Becker, and Jane (1968) have compared the medial lemniscus of *Erinaceus europaeus*, *Tupaia glis*, *Nycticebus coucang*, and *Saguinus oedipus* (marmoset). The major difference between *Erinaceus* (hedgehog) and the other species is in the progressive restriction of diencephalic terminations to the ventral posterior nucleus in the tree shrew, loris, and marmoset, as opposed to a wider distribution to other nuclei in the hedgehog.

Mesencephalon

The anterior colliculi of Tupaia remain relatively large, despite advances in the striatal cortex. These structures are relatively larger in tupaiids than in any other mammal, with the possible exception of the "flying lemur" (Cynocephalus, order Dermoptera). This is a primitive feature, in view of the great size of these structures (as optic lobes) in reptiles. As in many non-primate mammals, visual function at this level remains important (Le Gros Clark, 1959).

Von Tigges (1966) found that 80 per cent of retinal fibers reach the anterior colliculus; the other 20 per cent terminate in the dorsal nucleus of the lateral geniculate body. This demonstrates clearly the persisting dominance of visual function by the midbrain.

Feremutsch (1965) had made a preliminary study of the anterior colliculus in Tenrec ecaudatus, Tupaia glis, Blarina brevicauda, and certain primate species.

In *Tenrec ecaudatus*, the anterior colliculus extends well into the thalamic region, as in *Tupaia*, but to a lesser degree. Cells of the anterior colliculus show ill-defined stratification in *Tenrec*. In *Blarina brevicauda* arrangement into strata externum, intermedium, and internum is better defined. The overall structure is more like that of *Tupaia* or *Microcebus* than like that of *Tenrec*. *Tupaia glis* displays the laminated structure very nicely. As in Cercopithecidae, Pongidae, and *Homo*, the three strata can be clearly distinguished (Feremutsch, 1965).

Among Prosimii, only *Microcebus murinus* resembles *Tupaia*. Strata intermedium and internum are not sharply divided, however. *Lemur macaco* and *Loris tardigradus* show the three strata, if one looks carefully (Feremutsch, 1965).

Le Gros Clark's (1926b) comparative study of the mammalian oculomotor nucleus showed a very simple pair of lateral nuclei in *Erinaceus*. There is no differentiation of a recognizable Edinger-Westphal nucleus. *Macroscelides* is similar, except for the addition of a distinct Edinger-Westphal nucleus like that of *Tupaia*. In *Tupaia* the whole oculomotor nucleus is more elaborate. While the small cells of the Edinger-Westphal nucleus are not sharply circumscribed, the cluster is quite recognizable. The large-celled lateral nuclei are distinctly subdivided into dorsal, ventral, and paramedian groups. Although this pattern represents a definite advance over *Erinaceus* and *Macroscelides*, it is still a simple plan, detectible in the oculomotor nuclei of other mammals. With increasing elaboration of the nucleus in higher Primates and some other mammals, this arrangement of three longitudinal cell groups is progressively obscured.

The pattern in *Cynocephalus* is indicative of a trend in the direction observed in *Tupaia*. *Sciurus* is similar to *Tupaia*, except for certain differences in disposition of the parts of the oculomotor nucleus (Le Gros Clark, 1926b).

The Edinger-Westphal nucleus of *Nycticebus* and *Galago* remains relatively undifferentiated and poorly circumscribed. It is more conspicuous in *Tarsius*, becoming very distinct and separable into two cell groups in *Hapale* and *Macacus*. It reaches its peak in anthropoids, especially in man. Such a small-celled element, rather diffuse in outline, is found in a number of other mammals studied, including Pinnipedia and Cetacea (Le Gros Clark, 1926b).

Rhombencephalon

The cerebellum is rather poorly developed in tupaiids, being of a simple, generalized mammalian type. Its convolutional pattern, however, is more complex than that found in *Microcebus* (a primitive lemur). *Tarsius*, and insectivores (*Macroscelides*) of comparable size (Le Gros Clark, 1959).

Cell counts of the superior olivary complex in tree shrew (*Tupaia minor*), marmoset, squirrel monkey, and gibbon disclose regression of the lateral nucleus and nucleus of the trapezoid body, as compared with the medial nucleus, among these primates, in the order named (Sehmsdorff, 1966).

Corticospinal Tracts

Corticospinal tracts are found mainly in the dorsal funiculi of monotremes, marsupials, edentates, and rodents (Jane, Campbell, and Yashon, 1965).

Bautista and Matzke's (1965) study of the corticospinal tract of opossum shows the upper regions to be similar to other mammals down through the level of the pyramidal decussation. It then descends, however, in the dorsal funiculus of the entire cervical spinal cord. Fibers terminate at the base of the dorsal gray column. The corticospinal fibers show a rather broad area of origin. In marsupials the corticospinal tract has barely made its phylogenetic appearance. The degree of cortical influence over motor control appears to be slight.

Three insectivores (Erinaceus, Talpa, and Scalopus) show uncrossed ventral tracts. (There is no information on elephant shrews.) Crossed dorsal pyramidal tracts are not characteristic of insectivores (Campbell, 1966).

Jane, Campbell, and Yashon (1965) made a study of corticospinal tracts in Tupaia glis. The decussation in the medulla is apparently incomplete. Some individuals show a small bundle passing into the ipsilateral tract. Corticospinal fiber bundles are found in the dorsal funiculi, extending downward only to the mid-thoracic level of the spinal cord. The distribution of the terminations of the corticospinal fibers in the gray matter is only to the dorsal horn and intermediate zone, with none to the ventral horn.

Shriver and Noback (1966) studied the cortical projections to the brain stem and spinal cord in Tupaia glis by producing lesions in frontal and parietal cortex. Uncrossed terminations are found in the reticular formation of the entire brain stem. At spinal cord level, two pathways of degeneration occur: (1) large crossed dorsal tracts (throughout the cord), (2) small uncrossed dorsal tracts (in cervical segments only). The majority of terminations of these corticospinal fibers are in the dorsal horn of the gray matter, with a lesser number in the zona intermedia.

Cortical influence on cranial and spinal motor nuclei in tree shrews is therefore limited to the phylogenetically older "indirect" projections to internuncial neurons located in the reticular formation of the brain stem and in the dorsal horn of the spinal cord. The more advanced "direct" projections have not been added (Shriver and Noback, 1966).

In all Primates observed, most corticospinal fibers decussate to form the lateral corticospinal tracts, located in the lateral funiculi of the spinal cord, and extending the length of the cord (Shriver and Noback, 1966).

Nycticebus, the only prosimian examined, shows complete decussation. Fiber terminations are most numerous at the base of the dorsal horn and the intermediate gray column, with some fibers extending into the ventral horn (Shriver and Noback, 1966).

The terminal distribution of corticospinal fibers within the gray matter of the spinal cord of higher Primates is to the dorsal horn and intermediate zone, as well as to the ventral horn (Shriver and Noback, 1966).

Campbell (1966) stated: "As far as is now known, the localization of the major crossed corticospinal tract does not appear to vary within the same order, although it does vary from order to order." The corticospinal system of *Tupaia* differs from all known primates and insectivores. It cannot simply be regarded as primitive mammalian in type.

Peripheral Nervous System

There is one recorded feature in which *Tupaia* is transitional from generalized mammals to higher Primates: this is the innervation of the infrahyoid musculature. In general, among mammals, these muscles are supplied by the descending ramus of nervus hypoglossus and the descending cervical nerve (from upper cervical spinal nerves). In *Tupaia*, as in monotremes, marsupials, and most insectivores, this innervation includes cervical segments I and II (only the first cervical segment in *Sorex araneus* and *Erinaceus albiventris*). In *Lemur macaco* and all higher Primates observed, cervical segments I, II, and III are involved. In Prosimii and *Tupaia javanica* hypoglossal fibers supply only musculus thyrohyoideus, all other infrahyoid muscles being supplied by cervical nerve fibers. In Simiae all infrahyoid muscles are supplied by the first three cervical nerves (Fieandt, 1914).

Skeletal System--Axial Division

Skull

The similarity between Tupaiidae and Macroscelididae in development of the chondrocranium is striking (Henckel, 1928; Roux, 1947). From his investigation of the development of the macroscelidid skull, which resembles that of Tupaiidae very closely, Roux (1947) was convinced that it would be impossible for a primate skull to develop from this type, already on an "Insectivore line of specialization." Seemingly close affinities displayed by adult skulls of tupaiids and lemuroids are due, for the greater part, to parallel modifications resulting from their arboreal habits. Roux (1947) believed that the Menotyphla became separated from the primitive insectivore stem very early, to develop along a divergent line.

Broom's (1915) study of the vomeronasal organ (of Jacobson) indicated that the morphology of the associated cartilages are of value in determining affinities among mammals. The structure is almost the same in members of diverse orders. Since the arrangement of these cartilages is complex, Broom (1915) concluded that similarity indicates common origin rather than independent convergent variations.

Among Mammalia, Broom (1915) found two principal types: (1) the primitive (marsupial) type, representing a simplification of the monotreme organ, and retained in rodents with slight modification; (2) the higher (eutherian) type, found in *Lemur*, ungulates, carnivores, *Procavia*, some bats, and some insectivores.

Broom (1915) found that the vomeronasal (supporting) cartilages of *Tupaia* are very similar to those of *Macroscelides*, with differences being no greater than are found in different families of diprotodont marsupials or of artiodactyls. Both closely resemble polyprotodont marsupials and *Perameles*. They differ in almost every respect from *Gymnura*, an erinaceid insectivore. *Gymnura*, almost identical with *Erinaceus*, also agrees well with most Eutheria. Thus, Broom (1915) proposed that Menotyphla constitute a distinct order, closely related to marsupials, and showing little affinity with the "more typical Insectivores."

In general form, the tupaiid adult cranium has rounded contours, although a sagittal crest is present in *Urogale* (Lyon, 1913; Le Gros Clark, 1925). In showing broad convexity of the cranial roof between the orbits, Gregory (1910) found Tupaiidae differ widely from any Lipotyphla and approach Lemuroidea. Saban (1956-1957) regarded the tendency to increase the size of the cranium relative to the face in the same way.

Based on his study of development of the nasal skeleton, Spatz (1963) found the seeming reduction of the incisura pretrabecularis, in Tupaia, indicative of greater resemblance to Prosimii than to Insectivora. This semicircular notch of the lower border of the nasal septum marks the rostral end of the trabecular portion of this septum. Well developed in Insectivora, this incisure is scarcely perceptible in Tupaia glis, and completely lacking in Prosimii. The loss may be correlated with reduction in the olfactory apparatus.

Tupaia and Lemur, as opposed to Lipotyphla, have only two ectoturbinal bones (Le Gros Clark, 1925; Gaughran, 1954; Saban, 1956-1957; Sharma, 1958). Reduction of the nasal fossae, anterior nasal orifices, and choanae in Tupaia and Lemur are likewise correlated with diminution of olfaction (Saban, 1956-1957).

The presence of palatal vacuities is regarded as a primitive, metatherian feature of tupaiids (Le Gros Clark, 1925); Dendrogale, however, lacks such palatal fenestration (Davis, 1938).

The pattern of differentiation of foramina (for nerves and blood vessels) on the skull base resembles that of prosimians (Le Gros Clark, 1925). The presence of malar foramina was described by Le Gros Clark (1925) as a primate feature.

Observation of the basicranial axis shows some similarities between tupaiids and lemuroids. Le Gros Clark (1925) correlated a degree of flexion of the face on the basicranial axis in the ethmoid region with reduction in size of the olfactory bulbs. A study by Hofer and Spatz (1963) on embryonic and neonatal heads of representative primates, including *Tupaia glis* and *Lemur*, showed that the kyphosis at the base always lies rostral to the sella turcica.

The plane of the foramen magnum in tupaiids is somewhat depressed from the more primitive vertical position. This has been correlated by Le Gros Clark (1925) with the development of occipital poles on the cerebral hemispheres in tupaiids and lemuroids. It may also be functionally related to the common assumption of the sitting posture in these groups.

The presence of a tympanic wing or process of the alisphenoid bone is regarded as a metatheroid feature (Gregory, 1910; Le Gros Clark, 1925). Although this process is much reduced in *Tupaia*, it retains more of the posterior concavity, characteristic of primitive marsupials, in *Ptilocercus* (Gregory, 1910).

The form of the ectopterygoid fossae, on the other hand, was found by Gregory (1910) to resemble that of Lemuroidea.

The presence of an alisphenoid canal is another primitive metatherian trait (Le Gros Clark, 1925). This canal persists in scattered, primitive placental groups, including most Insectivora and many Carnivora (van der Klaauw, 1931; van Valen, 1965). This foramen pierces the base of the pterygoid flange (external pterygoid process) of the alisphenoid bone. In _Tupaia glis_ the internal maxillary artery passes through it along a short portion of its course.

Ancient mammal-like reptiles had an enclosed orbit and a wide-angle optic axis. This was evidently retained in early marsupials. (Later mammal-like reptiles and all modern marsupials have had an open orbit.) Early placental mammals also had an open orbit, as did some early lemuroids; yet tree shrews have an enclosed orbit, as in modern primates generally. Primates, with the exception of tree shrews, possess narrow-angle optic axes. With a more complete fossil record, this sequence will be of greater phylogenetic interest (Prince, 1956).

Le Gros Clark (1925) and Saban (1956-1957) pointed to the considerable forward rotation of the orbits, especially in _Ptilocercus_, as indicative of a tupaiid link with _Lemur_. An index, based on the angle between optic axis and the sagittal plane, is intermediate, for _Tupaia_, between insectivores and primates. Saban found the same to be true of the interorbital distance in relation to the breadth of the face. A broad interorbital region is a primitive characteristic for Eutheria. Van Valen (1965), however, did not find the orbits of *Tupaia* to be relatively more anterior and close to each other than in other primitive mammals. He did concede that the snout is somewhat shorter than usual.

Saban (1956-1957) believed that there are a number of secondary effects to be correlated with forward migration of the orbits. These, he said, result in greater similarity between Tupaiidae and Lemuridae than between Tupaiidae and Insectivora generally. These secondary skull modifications are as follows:

1. The malar bone is extensively involved in forming the orbital margin.

Van Valen (1965) regarded the posterior extension of the malar bone as a primitive feature, however.

2. The malar bone possesses a frontal process that, together with the frontal bone, completes the posterior bony wall of the orbit.

Although it is agreed (Gregory, 1910; Le Gros Clark, 1925) that a well-developed postorbital bar involving frontal and malar bones is typical of

Primates, van Valen (1965) points out that this bar is variable in Ptilocercus, and is apparently not primitive in Primates. It is absent in Plesiadapis. Postorbital bars, although differing in constitution, have developed in some other placental orders.

3. A malar foramen is present.

This statement is inaccurate. The foramen is minute in most tupaiids (Le Gros Clark, 1925). Further, as van Valen (1965) noted, this foramen is absent in Plesiadapis and in a number of Recent prosimians.

4. The lacrimal sulcus and infraorbital canal (the anterior openings of the orbit) have been shifted toward the external orbital margin. The optic foramen has been elevated to a position above the sphenoidal fissure.

Van Valen (1965), on the contrary, maintained that the lateral positions of the lacrimal foramen and infraorbital canal are primitive features.

In Ptilocercus and many prosimians, the optic foramen does not lie above the sphenorbital fissure. Erinaceids, on the other hand, do show the superior position of the optic foramen (van Valen, 1965).

5. The medial orbital wall, in contrast to Insectivora, displays broad palato-frontal contact, but no sutural contact between the temporal and parietal

bones.

Van Valen (1965) argued that the extension of the palatine to the lacrimal bone and the extensive frontopalatine suture are primitive features. Groups in which they are lacking, however, include *Plesiadapis*, *Adapis*, and *Pronycticebus* among fossil forms, as well as *Daubentonia* of Recent times.

In commenting further on the nature of the inner orbital wall, van Valen (1965) emphasized the following observations:

1. Exclusion of the squamosal and parietal bones is evidently primitive.
2. Although Evans (1942) stated that the malar-lacrimal contact is shared by tupaiids and prosimians, this feature is primitive and shows variation within the two groups.
3. Subdivision of the lacrimal bone into facial and orbital parts (Gregory, 1910) is not clearly defined in *Ptilocercus* and is apparently primitive.
4. An os planum, although present in a *Tupaia* embryo described by Carlsson (1922), is not found in the adult. It is found in a number of mammals. It is limited, among prosimians, to certain species only.
5. Although the lacrimal foramen pierces the lacrimal bone immediately anterior to the orbital margin in tupaiids and lemurs (Gregory, 1910), this feature shows

much variation among prosimians, as among Eutheria generally.

6. While a supraorbital foramen is present in Tupaia, it does not appear in Ptilocercus, Plesiadapis, or in many Recent Prosimii.

7. It is true that tupaiids and prosimians have larger orbits than most primitive mammals; yet such enlargement has also occurred in a number of other eutherian groups.

Another area of current dispute between van Valen (1965) and long-accepted authorities on tree shrews involves the auditory ossicles. Doran (1879) wrote a treatise on the variation of these bones among mammals. He stated that the malleus of Tupaia "differs from that of any other insectivorous mammal" and resembles that of Primates; neck, anterior process, and pars brevis are absent. In Madagascan lemuroids these parts are slightly developed. The malleus of Tarsius also lacks a neck. He concluded that the tupaiid malleus most closely resembles that of such lower primates as some lemurs and marmosets, especially in the shortness of processus gracilis.

As in many monkeys and lemurs, the tupaiid incus was described by Doran (1879) as having a high, narrow body.

Although the presence of a bony canal in the stapes is shared with Lipotyphla and prosimians, the stapedial crura are straight in tupaiids but curved in Lipotyphla (Doran, 1879).

In general, Doran (1879) found the ossicles to differ from any of the varied forms observed among Insectivora.

After examination of the published figures and descriptions (Doran, 1879; Le Gros Clark, 1926a; Werner, 1960), van Valen (1965) failed to see any special resemblance to Primates. In addition, van Valen (1965) noted differences between the ossicles of *Tupaia* and *Ptilocercus*. The processus gracilis, which is well developed in *Tupaia*, is lacking in *Ptilocercus*. Van Valen (1965) concluded that the similarities of tupaiids to Primates is no greater than to other Eutheria.

The Leptictidae had an ear region closely resembling the basic type from which tupaiid and primate types must have developed in Cretaceous to Tertiary times (McKenna, 1966).

Werner (1960) emphasized the value of the middle and inner ear features in determining phylogenetic relationships. Their recessed and protected position removes them somewhat from external environmental influences. Of course, neighboring structures of more direct adaptive significance, such as jaws and brain, must have modified their development.

Although the middle ear enclosure arises separately from the cranium, its bony elements either are part of the cranial wall or merge with it secondarily.

Anterior to the tegmen tympani, the alisphenoid bone contributes to the wall of the middle ear cavity in _Tupaïa_ and in young _Perodicticus_ individuals. After the later fusion with the petrosal bone, evidence of alisphenoid participation is no longer demonstrable (Werner, 1960).

The ventral (jugular) wall of the middle ear cavity varies among primates. In Lemuroidea, it is formed by a thin and arched bony plate, the bulla ossea.

In Tupaiidae, the greater part of the bulla wall develops from a separate endochondral bone, the os bulla or entotympanicum, apposed to the petrosal bone below, and to the cochlear region medially. The tree-shrew bulla evidently is a compound structure containing some additional minor contributions. There is a small contribution from the alisphenoid, and perhaps from the basisphenoid bone as well (van der Klaauw, 1929). Saban (1956-1957) denies this, finding that the presence of the latter is typical of insectivores generally, but not of Tupaia and Lemur. Spatz (1966) found slight supplementation of the bulla wall by a small processus tympanicus petrosi caudalis in Tupaia glis.

All fusions of the greatly expanded entotympanicum with other skull elements are secondary. Saban (1956-1957), however, argued for absence of an entotympanicum in Tupaia and Lemur, believing that the bulla floor is formed solely by an expansion of the petromastoid region of the temporal bone.

The os entotympanicum was regarded by Werner (1960) as a new acquisition among mammals. Spatz (1966) agreed with this, and argued for affinity between tupaiids and Malagasey lemuroids, based on belief that the prosimian bulla was derived from a tupaiid bulla by a primordial fusion of entotympanicum with petrosum. He also noted similarity in the overall form of the bulla; van Valen (1965), however, did not find greater similarity between these bullae than is commonly found between unrelated groups of placental mammals.

Van der Klaauw (1929) noted that although a free entotympanic bone is present in Menotyphla, it is not found in any modern Lipotyphla or in the ontogeny of the Primates.

The early fusion of entotympanicum to

petrosum has been the basis of continuing controversy through the present century. If, as van Kampen (1905) suggested, the entotympanic bone represents merely the expanded and secondarily independent tympanic wing of the petrosal bone observable in many marsupials and insectivores, then the difference in bulla formation of Menotyphla and Lipotyphla is a difference of degree, not of kind. There is no doubt that the great difference now existing implies a long period of separation between Menotyphla and Lipotyphla.

Van der Klaauw (1929) demonstrated that in Macroscelididae the bulla is formed by the two entotympanic bones (caudal and rostral), supplemented by alisphenoid, basisphenoid, petrosal, and ectotympanic bones.

McKenna (1966) pointed out that in the course of tupaiid evolution, the medial border of os entotympanicum apparently has fused (in adult) to the os petrosum. Some traces of such fusion do exist in adult tupaiids. In juvenile tupaiids (e.g., Tupaia glis modesta), the entotympanic portion of the bulla remains long separated from the petrosal bone. The adult fusion of entotympanicum to petrosum is thus believed to have been a relatively recent phylogenetic event among tupaiids. It is on the basis of the adult structure that the tupaiid bulla is often erroneously considered to be an outgrowth of the petrosal bone, even as in Malagasey lemurs and other primates.

Van Valen (1965) has assembled much evidence against tupaiid-primate affinity based on bulla composition. He confirmed the virtually exclusive contribution of an os entotympanicum. He contradicted Saban's (1956-1957) statement that no suture is found lateral to the carotid foramen (in os petrosum). In almost all young skulls (and even a few presumably mature ones) observed by van Valen (1965), such a suture is present. Since ossification of os entotympanicum evidently begins anteromedially (near the pharyngotympanic tube), van Valen (1965) believed this bone is homologous to the anterior entotympanic bone described by van der Klaauw (1929).

In lemurids and lorisids, on the contrary, the major portion of the bulla grows out (ontogenetically) from the medial aspect of the os petrosum (van Kampen, 1905; van Valen, 1965). Ossification here is not initially limited to the anteromedial region, but occurs medially throughout the length of the bulla. The medial portion of the bulla is evidently derived from both mastoid and petrosal regions, at least in lorisids. Van Valen's (1965) evidence indicated this probably is also true for Lemur.

Van der Klaauw (1931) pointed out that bullae may develop from any bone or cartilage adjacent to the middle ear region, in one or another mammalian group; bullae derived from a given element have developed independently, by convergent evolution, a number of times. Thus, even if the bullae of tupaias and lemurs are homologous, this alone would not be conclusive evidence of proximate common ancestry.

According to Gregory (1910), the true tympanic bone remains as a delicate ring inside the entrance of the bulla in both Tupaiidae and Lemuriformes. Hill (1953b) noted that in all Malagasey lemurs, including Daubentonia, the annulus tympanicus, although not involved in bulla formation, becomes enclosed to lie free within the bulla during development. This condition is described as unique among living mammals, except for Tupaiidae. He noted that it is also found in the fossil Adapidae and Plesiadapidae. McKenna (1966) added fossil Leptictidae to the list.

A free tympanic ring is certainly primitive; yet, as van Valen (1965) emphasized, no direct process can be envisaged by which a Malagasey lemuroid bulla could develop into one similar to that of Perodicticus, the bulla of the latter being comparable to the bullae of Plesiadapis, Tarsius, and anthropoids. The problem is to get the tympanic element incorporated into the already completed bulla surrounding it. One ontogenetic possibility, suggested by van Valen (1965), involves failure of the petromastoid bulla to grow out over the tympanic ring. This, however, would require an abrupt transition between the two adult conditions. Some functional disturbance would be likely. In searching for possible intermediate stages, van Valen (1965) observed that, at times, old Lemur individuals display calcification, and possibly ossification, of the annulus membrane. Such occurrence, ontogenetically, could lead to lateral expansion of the tympanic bone, following incorporation into the bulla.

Tupaia has been said to differ widely from Lipotyphla and to resemble Malagasey lemurs in the shape and position of the ectotympanic bone (van Kampen, 1905). Gregory (1910) noted that the ectotympanic bone extends laterally to form a very short external auditory meatus. Although most conspicuous in Catarrhinae and Hominoidea, this development also occurs in Loris and Nycticebus. Some degree of such development variably occurs among Insectivora (Saban, 1956-1957).

Among the features of the bulla listed as similarities between Tupaia and Lemur are the following (Saban, 1956-1957):

1. The orifices (carotid foramen, stylomastoid foramen, orifice of pharyngotympanic tube) are peripherally located.

2. The septa delimiting the diverticula of the bulla are arranged in the same manner.

Van Valen (1965) stated that similar septa commonly develop even in non-homologous bullae. Lyon (1913) had indicated that these septa are lacking in Ptilocercus.

3. The counterpart of the basisphenoidal diverticulum is absent; yet it is always present in Insectivora.

4. The hypotympanic sinus is large.

Van Valen (1965) maintained (citing van der Klaauw, 1931) that such an inflated bulla is a common evolutionary development among mammals.

5. A bony canal for the pharyngotympanic tube is present here, but absent in Insectivora.

Yet, such a bony covering is a common evolutionary development (van der Klaauw, 1931).

6. There is early synostosis of the fissure of Glaser. In Insectivora, the fissure remains widely

open.

7. The epitympanic recess has straightened to become integrated with the interior of the bulla. This is correlated with a realignment of the tympanic framework.

Van Valen (1965) considered this relatively internal position of the epitympanic recess as a primitive feature. It also appears in some other mammalian groups.

8. The recessus meatus is enlarged.

It is likewise enlarged along other mammalian lines, according to van Valen (1965).

9. Portions of the vestibular complex display similar interrelations.

10. The inferior petrosal (venous) sinus opens into the internal jugular vein. Among Insectivora, this opening always leads into the lateral sinus.

Extracranial passage of the inferior petrosal sinus is also to be found in marsupials, according to van Valen (1965).

11. The petro-squamous sinus is of very large diameter.

Van Valen (1965) regarded this feature as being probably primitive, although rather variable.

Saban (1956-1957) measured angles of inclination of the petrous temporal bone. These indicated that tupaiids are about equidistant from most Insectivora on the one hand, and from Primates on the other. He related these angles to the tilting of the occiput, presumably the result of increased brain size. Van Valen (1965) pointed out, however, that since the brain is relatively small in *Plesiadapis*, the greater size found in Recent tupaiids and Recent lemuroids has probably arisen independently.

A mastoid region of the petrous temporal bone is not yet distinctly set apart in tree shrews. There are no air spaces here. Lemuriformes show less pneumatization of the expanded petrous and squamous temporal regions than Lorisiformes (Gregory, 1910; Werner, 1960).

Dentition

McKenna (1966) noted the scarcity of early Paleocene insectivore remains, with which early primates must be compared. He also pointed out that Eocene deposits of southern Asia and Borneo, which may be expected to contain fossil tupaiids, have not been searched carefully, using appropriate collecting techniques. Even so, for thin-skulled inhabitants of tropical forests, teeth will probably remain the best index to the phylogenetic position of tree shrews.

Although available evidence indicates that living adult tupaiids show more similarity to living adult Malagasey lemuroids than to living adult insectivores, Primates obviously arose from fossil, not living, insectivores of late Cretaceous and early Tertiary times. A later insectivore radiation gave rise to modern Lipotyphla. Even in the Eocene epoch, leptictids, as well as moles, shrews, and hedgehogs, still resembled tupaiids in dentition and certain features of the ear region. Leptictid fossils date from Cretaceous to Oligocene times (McKenna, 1966).

Van Valen (1965) observed that the evolutionary path from Procerberus (the most primitive known eutherian mammal, dating from the late Cretaceous period) to Adapisoriculus (accepted as leptictid) does not closely resemble that leading to Paleocene Primates. There is greater similarity to trends leading to primitive erinaceoids. Recent tupaiids agree well with the trends exhibited by Adapisoriculus of the Paleocene epoch.

The tritubercular teeth of Adapisoriculus and of Recent tupaiids more closely resemble those of primitive forms of Didelphidae and Dasyuridae than those of any Recent or extinct placental mammal (van Valen, 1965).

The primitive condition of the upper molar tooth, with a raised trigone and a talon basin, persists only in Tarsiidae, among Prosimii (Napier and Napier, 1967).

In dentition, there appears to be greater similarity between Adapisoriculus and either Tupaia or Ptilocercus than there is between the latter two genera; thus van Valen (1965) would place all three genera in the family Tupaiidae.

The lower molars of Tupaiidae are also primitive in being tuberculosectorial (Gregory, 1910), with sharply pointed cusps and enlarged styles. All prosimian families, except Tarsiidae, have modified this trigonid to produce a quadricuspid tooth (Napier and Napier, 1967).

Adapisoriculus, Plesiadapis (most primitive known primate), and Anagale (questionable Oligocene tupaioid) all retained the full placental complement of teeth:

$\frac{3-1-4-3}{3-1-4-3} = 44$ (Le Gros Clark, 1959; van Valen, 1965).

In modern tree shrews, the dental formula is as follows: $\frac{2-1-3-3}{3-1-3-3} = 38$. This represents less reduction than in any living primate. Reduction is common in many mammalian orders, including Insectivora. No primate has more than two incisors in the lower jaw. In tupaiids, the third lower incisor is reduced, having almost disappeared in Urogale.

Absence of the first premolar teeth is also frequently observed among insectivores. Reduction of canine teeth, typical of insectivores, also occurs in many primate groups.

The lower incisors of tupaiids are somewhat procumbent to form a comb or scraper. Generally, the lower canines are not involved in this formation. In one genus, Anathana, the canine is also quite procumbent and may be interpreted (Buettner-Janusch, 1966) as related to an earlier stage in evolutionary development of the tooth-comb found in modern Lorisidae, Indriidae, and Lemuridae. In these prosimian families the lower incisors, together with the canines, form a closely packed series of horizontally projecting teeth. (Certain Cebidae also show moderate procumbency of the lower incisors.)

This specialization of Tupaiidae and many Prosimii probably represents evolutionary parallelism. This feature was not present in any early Cenozoic prosimians. Ptilocercus has the tooth-scraper less well developed than in other tree shrews (Simons, 1962). Some lipotyphlous insectivores, such as Blarina brevicauda (short-tailed shrew), display "pronate" incisors (Gaughran, 1954).

Szalay (1968) has emphasized the primitive nature of transversely oriented preparacrista and postmetacrista for Metatheria and Eutheria. These are correlated functionally with a transverse shearing mechanism. This feature is not found in the earliest primate fossils. Leptictids show reduction of this feature; early primates show even less of it.

Mixodectids, with probable close leptictid ties and some similarities with Recent tupaiids and Adapisoriculus, differ considerably from the Eocene microsyopids, which are probably closely related to Paleocene prosimians (Szalay, 1968).

The dentition of Ptilocercus (most primitive living tupaiid) "does not greatly resemble the dentitions of primitive and early prosimians," according to Szalay (1968). Tupaiids completely lack conules. Strong, bulbous conules are present in microsyopids and early primate families (paromomyids, plesiadapids, and carpolestids); indeed Szalay (1968) would include microsyopids within the order Primates. He would not give leptictids the central position in relation to eutherian evolution that McKenna (1966) and van Valen (1965) have ascribed to them.

Vertebral Column

The numbers of vertebrae in the different regions of the tupaiid column is typical for primitive mammals (modal numbers: 7 cervical, 13 thoracic, 6-7 lumbar, 3 sacral, 25 caudal vertebrae). In this, Tupaiidae resemble prosimians more closely than insectivores. Correlated with climbing and leaping habits are the anteriorly directed lumbar parapophyses, shared with Macroscelididae and prosimians. The overall arched condition of the back, in Tupaiidae, is a primitive marsupio-placental condition (Gregory, 1910; Lyon, 1913; Le Gros Clark, 1926a; Davis, 1938; Schultz, 1961).

Sternum

In *Tupaia*, as in all prosimians and lower simians, the sternum is very slender. The length is comparable with prosimians and many insectivores and is probably a primitive mammalian feature (Gregory, 1910; Schultz, 1961).

Ribs

The number of sternal ribs lies within the prosimian primate range but probably approximates the primitive mammalian condition (Gregory, 1910; Davis, 1938; Schultz, 1961).

Skeletal System--Appendicular Division

It has been rather generally accepted that the most primitive marsupial and placental mammals were somewhat arboreal in habitat; thus the modern opossum (*Didelphis*) and the tree shrew would be close to these stem forms. Other authorities have pictured the most primitive mammals as terrestrial (Haines, 1958). In any event, tree-shrew limbs conform closely to primitive arboreal mammals generally. The length of the hind limbs exceeds that of the fore limbs. Limb-joint mobility closely resembles that of plesiadapid Primates of the Paleocene epoch (Le Gros Clark, 1959).

Anterior Appendages

The tupaiid clavicle permits a full range of prehensile activity (Lyon, 1913; Le Gros Clark, 1926a).

In Tupaiidae the humerus is approximately equal in length to the forearm; in Lipotyphla the humerus is relatively shorter (Gregory, 1910; Le Gros Clark, 1926a).

Primitive mammalian features of the tupaiid humerus include the low, elongated deltoid crest, the short and low supinator crest, as well as the entepicondylar foramen and pronounced entepicondyle characteristic of *Ptilocercus*. In *Didelphis*, *Lemur macaco*, *Erinaceus*, and *Sciurus*, the deltoid and supinator crests are relatively more sharply defined. *Anagale*, the questioned tupaioid, resembles primitive lemuroids more closely than the typical tupaioids in having a stronger supinator crest (Gregory, 1910; Carlsson, 1922; Simpson, 1931).

Primate features of the distal tupaiid humerus include the distinct separation of the capitellum from the trochlea by a low external lip on the latter (Le Gros Clark, 1926a). As in Lemuridae, the trochlea and capitulum of Tupaia lie side by side in a transverse plane, indicative of a primitive position of radius and ulna; Erinaceus differs in this respect (Carlsson, 1922).

Radius and ulna tend to remain distinct, although there may be a varying amount of ossification extending into the interosseous membrane; this may be correlated with leaping habits (Lyon, 1913; Carlsson, 1922; Le Gros Clark, 1926a).

Overall, the carpus of Tupaiidae is morphologically intermediate between that of lipotyphlous Insectivora and Lemuroidea.

In Tupaiidae and Lemuridae, as in marsupials and most lower placental mammals, the dorsal surface of the lunate bone makes broad contact with the hamate bone. The area of contact is reduced in Erinaceidae and Sciurus (Carlsson, 1922).

A free os centrale, also regarded as a primitive mammalian feature, is found in Tupaiidae

and Lemuridae, as well as in *Sciurus*, *Talpa*, and many other Lipotyphla; it is absent in *Erinaceus* and all marsupials (Carlsson, 1922).

As in *Sciurus*, Erinaceidae, and *Setifer* (a primitive tenrecid insectivore), the navicular and lunate bones are united in *Tana tana* and *Tupaia* to form a broad, shallow area. Scaphoid (navicular) and lunate bones are separate, however, in *Ptilocercus* and *Dendrogale*. This latter condition is both more specialized and more lemurine (found in Lemur) (Le Gros Clark, 1926a; Davis, 1938).

In Marsupialia the capitate and hamate bones together are larger than navicular and lunate bones; the size relations are reversed for most primitive placental mammals (Gregory, 1910). Yet, *Tupaia* and *Lemur* resemble Marsupialia in this respect, while *Sciurus* and *Erinaceus* resemble primitive Eutheria (Carlsson, 1922).

Posterior Appendages

In tree shrews the os innominatum generally shows the form characteristic of primitive arboreal mammals (Gregory, 1910).

The ilium of *Tupaia* and *Ptilocercus* is more spatulate than in elephant shrews, thus being further differentiated from the simple trihedral shape observed in *Didelphis*. In *Tupaia* the sacral surface

is much wider than the iliac surface. An enlarged sacral surface (for ligament and muscle attachments) is found in all Lemuroidea and monkeys. The relative width of the ilium increases but little in the lower Lemuroidea (*Galago*, *Microcebus*, *Cheirogaleus*) (Straus, 1929).

The overall height-width index of the ilium in Tupaiidae resembles *Lemur*. As in *Lemur*, the iliac surface in tupaiids is absolutely widest in the lower posterior part, definitely narrowing toward the crest, where pubic and acetabular borders are confluent (Straus, 1929).

The ilium of *Ptilocercus* is more primitive than in *Tupaia*, showing less concavity of the lateral surface, and a simple rod-like form. Lipotyphlous ilia are even more rod-like and non-spatulate. The gluteal surface is nearly flat in *Rhynchocyon* and *Macroscelides*. Iliac surfaces, in these elephant shrews, are directed ventrolaterally, as in opossum (Straus, 1929).

The acetabular border of the ilium is straight in opossum, almost straight in elephant shrews, but somewhat concave in tupaias. Generally, this border remains straight in Lemuroidea. It is quite concave, however, in *Lemur*, *Cheirogaleus*, *Lichanotus* (woolly lemur), *Propithecus*, and *Indri*

(Straus, 1929).

There is a prominent antacetabular spine (anterior inferior iliac spine) in Tupaia. This spine is not found in most marsupials and lipotyphlous insectivores. While large in all Menotyphla, the antacetabular spine shows much variation among Prosimii, from a trace to considerable enlargement (Straus, 1929).

The sacroiliac articular surface in Menotyphla, Lemuroidea, and monkeys resembles that of lower mammals generally. The surface takes a shallow U shape, with ventral arm somewhat the longer (Straus, 1929).

Among primitive mammals it is the rule to have only one or two (sacral) vertebral segments articulating with the ilium. Marsupials show one or two. Lipotyphla show one to three. Among Menotyphla, Tupaia and Rhynchocyon have just one, Ptilocercus and Macroscelides have two. The variation among Lemuroidea ranges from one to three (Straus, 1929).

Straus (1929) concluded that minor changes could transform a tupaioid ilium into a lemuriform ilium. The simplest change would lead to Lepidolemur and Lemur, and thence to Indris and Propithecus. If this did occur, however, one must explain the apparently more primitive ilia found in most other

Lemuroidea. If, as an alternative hypothesis, one assumes evolution of the tupaioid ilium in parallel with Lemur and allies, one must search for the ancestral lemuroid type among other Menotyphla or related forms. The fossil evidence remains inconclusive.

The symphysis in Menotyphla (Tupaiidae and Macroscelididae) involves union of both pubis and ischium. This is a primitive mammalian condition. Lipotyphla show some degree of reduction, or even complete absence, of such a symphysis. Prosimii have a strictly pubic symphysis (Carlsson, 1922; Le Gros Clark, 1926a; Davis, 1938).

The gluteal ridge ("third trochanter") of Tupaia is prominent, extending farther distally than the lesser trochanter. This is a primitive condition shared with Sciurus and Didelphis. In Erinaceus, it is represented by a crest (Gregory, 1910; Carlsson, 1922).

Another primitive feature of Tupaia is the shallow patellar trochlea (Gregory, 1910).

Having tibia and fibula completely separated throughout their length is a primitive feature shared with Didelphis and Prosimii (except Tarsius). Fusion is constant in Macroscelididae (jumping forms) and is common among Lipotyphla (with many fossorial forms)

(Gregory, 1910; Lyon, 1913; Carlsson, 1922).

The lemuroid features of the tupaiid tarsus may be correlated with adaptation to an arboreal life. The strong malleoli are associated with subvertical facets on the astragalus. This arrangement is also found in *Sciurus* (Carlsson, 1922).

The broad confluence of the sustentacular facet with the navicular facet of the talus, in Tupaiidae, is also observable in *Lemur* and *Sciurus*; the facets are clearly set apart in *Erinaceus*. In *Tupaia*, as in *Lemur*, the ectal facet is the larger; the two facets are about equal in *Sciurus*. Since, in the primitive Marsupialia, the sustentacular facet is in continuity with that for the navicular bone, Carlsson (1922) felt justified in viewing this common feature of *Lemur* and *Tupaia* as a sign of genetic relationship.

The facet of metatarsal I for articulation with the entocuneiform bone is oblique and somewhat saddle-shaped in tupaiids. The obliquity is slight, however, in comparison with *Lemur*, in which the facet is turned medially for great opposability of the hallux (Carlsson, 1922; Buettner-Janusch, 1966).

The terminal phalanges of the pes in *Anagale* were flattened and spatulate. Since this resembles the condition in various advanced prosimians more closely than that of modern tree shrews, it has been thought that this fossil form would tend to lessen the morphological gap between tree shrews and lemurs (Simpson, 1931; Le Gros Clark, 1959).

Haines (1958) believed that the primitive placental hand was probably of the convergent type, in which the tips of the digits converge to lie close together in flexion upon the palm. This is still commonly found in reptiles, most insectivores (except burrowers and tupaiids), as well as carnivores. A clasping hand, as found in Didelphis among other marsupials, is used in climbing. The entire hand grasps the branch. A prehensile hand with opposable pollex is found in some marsupials, primates (including all lemurs), and (incipiently) in tupaias. Haines (1958) pointed out, however, that the opposability in tree shrews may have resulted from parallel evolution. Among the unique features may be noted the articulation of the trapezium with the scaphoid, centrale, and trapezoid bones. The trapezium also shows close ligamentous attachment to metacarpal II, and receives some fibers from the abductor pollicis longus muscle. The articular surface for the first metacarpal is saddle-shaped, although the articular cartilage and synovial cavity are continuous with those of the scaphoid. This peculiar type of opposability may have been superimposed on the clasping type of hand, Haines (1958) believed.

Whereas Haines (1958) thus regarded the Tupaiidae as too specialized (at least in the adult) to approach the basic mammalian stock, Steiner (1951) regarded Tupaiidae as the most primitive of living mammals, based on embryological study of the hand and foot skeleton of *Tupaia*. Steiner (1951) also believed it is the arboreal mode of life that "stamps" the adult structural organization of primates and tupaiids as well as the basic mammalian type. Among the features--paralleling many other mammalian features--first appearing in the basal cheiridial elements of theromorph reptiles are the elongated form of the first carpal and tarsal bones and a degree of opposability of the pollex and hallux. Steiner (1951) found that ontogeny of the tupaiid hand and foot skeleton demonstrates derivation of mammalian features directly from reptiles. He found all four centralia of primitive tetrapods present in the mammalian carpus. Overall, the embryonic skeleton of hand and foot is surprisingly similar to that of the lower tetrapods. The later deviations, generally regarded as typical mammalian features, manifestly are adaptations to an arboreal way of life, according to Steiner (1951).

Based on his ontogenetic study of the hand, Lorenz (1927) concluded that Tupaia is more primitive than, and probably not ancestral to, the Primates. Although the adult hand is narrow and adapted for "claw-climbing," the embryonic hand is broad and of a primitive "clasping-hand" construction. Primates (barring certain specialized "claw-climbing," "callosity-climbing," and brachiating variants) are still more or less clearly "clasping-hand climbers," with a relatively much broader adult hand than in Tupaia. The embryonic tupaiid hand approximates most closely (of any known living form) the primitive clasping hand of the hypothetical "climbing-creeping primitive mammal."

Napier (1961) classified primate hands as either "convergent" or "prehensile with pseudo-opposable or opposable thumbs." If an animal habitually picks up and holds food in one hand, Napier (1961) would regard it as having a "prehensile" hand. On this basis, the hand of Tupaia glis is considered to be "convergent." Despite some divergence of the thumb, the tree shrew does not usually pick up food in one hand; thus Tupaiidae would be the only Primates with convergent hands.

Napier (1961) pointed out that the considerable degree of divergence of the pollex indicated in

Eocene mammals need not imply opposability, for such divergence was a feature of primitive reptiles as well. The feature may be considered as pre-adaptive for later opposability.

Prehension, in Lemuriformes and Lorisiformes, shows some increase in complexity over Tupaiidae. In reaching for an object, most prosimians open the hand and then close the fingers around the object. Fingers are not simply flexed in one plane, as in *Tupaia*. The advancement here involves hand structure, rather than any improvement in nervous control; there is still no variability in prehensive pattern (Bishop, 1962).

Muscular System

In their studies of tupaiid musculature, Carlsson (1922) and Le Gros Clark (1924b) used the squirrel (*Sciurus*) as a kind of "control" to determine whether features peculiar to *Tupaia* among insectivores might be arboreal adaptations. There is also a difference in degree of arboreal activity among Tupaiidae. The small species, such as *Tupaia minor*, with relatively longer tails, are so arboreal as to frequent the higher branches of large trees; the larger species, such as *Tupaia ferruginea*, with short tails, tend to be "bush animals." Despite these differences among tupaias and squirrels, there are no corresponding differences in musculature; thus the primate-like features found in tupaias cannot be readily dismissed as secondary (convergent) adaptations to an arboreal life. The features in which Tupaia agrees with Lipotyphla and differs from Lemuroidea are generally regarded as primitive mammalian characters.

Muscles of the Head and Neck

In the head and neck region, features of Tupaia that have been regarded as more or less primitive and not shared with prosimians include the following:

1. Musculus temporalis is composed of three parts (Carlsson, 1922).

Although Årnbäck-Christie-Linde (1907) found three parts in Crocidura and Sorex, no separation into three parts could be demonstrated in Scalopus aquaticus by Gaughran (1954). The muscle shows three regions but is not split into three parts in Suncus murinus (Sharma, 1958).

2. Musculus digastricus has its bellies separated only by a thin tendinous intersection in Ptilocercus, although Tupaia shows a well-developed central tendon. The tupaiid digastric muscle joins that of the opposite side for a short distance in front of the hyoid bone (Le Gros Clark, 1926a).

Sharma (1958) pointed out that "this is one of the most variable muscles in the Insectivora." In *Suncus* (Sharma, 1958) and *Blarina* (Gaughran, 1954) a very delicate tendinous intersection is present. No tendinous inscription was observed in *Scalopus* or in *Talpa* (Gaughran, 1954). Thus, among insectivores, three types of musculus digastricus exist: (1) with tendinous intersection, (2) without tendinous intersection, and (3) with intermediate tendon. Tupaiidae alone, among insectivores, may have the type with intermediate tendon (Sharma, 1958).

The interrelations of the paired anterior bellies also is variable. In *Blarina*, the antimeres are attached by a fascial sheet. In *Talpa*, fibers of the left tendon run deep to those of the antimere. In *Scalopus*, anterior belly fibers interlace along the mid-sagittal plane with those of the antimere. This condition in *Scalopus* is regarded (Gaughran, 1954) as more primitive than that in *Blarina*.

3. Differentiation of a scalenus anticus muscle has occurred in *Tupaia*, although it is not yet distinct in *Ptilocercus* (Le Gros Clark, 1926a).

Musculus scalenus shows three distinct parts (ventral, medial, and dorsal), but all lie dorsal to the brachial plexus in *Blarina* and *Suncus* (Gaughran, 1954; Sharma, 1958). No distinct subdivisions are demonstrable in *Scalopus* (Gaughran, 1954).

4. The medio-ventral border of musculus platysma, although very poorly defined in *Ptilocercus*, does become definable in *Tupaia* (Lightoller, 1934).

5. The notoplatysma muscle (with origin posteromedial to the acromioclavicular joint) is well developed, but tracheloplatysma (with origin anteromedial to the acromioclavicular joint) is still lacking in *Tupaia javanica* (Lightoller, 1934).

Features of head and neck musculature indicative of primate trends are the following:

1. Musculus digastricus shows a well-developed central tendon in *Tupaia* (Le Gros Clark, 1924b).

2. Musculus scalenus anticus is differentiated in *Tupaia*, as in Lemuroidea (Le Gros Clark, 1924b).

3. The medio-ventral border of the platysma muscle is defined in *Tupaia* and lemurs (Le Gros Clark, 1924b).

4. Lightoller (1934) stated that all four groups he examined (*Tupaia*, *Hapale*, *Lemur*, and *Tarsius* species) show "the primate modification of the mammalian plan of facial musculature." This includes the extension of the naso-labial muscle into the medial frontal region, the presence of a superficial orbito-auriculo-labial musculature, simplification of the

retro-auricular musculature, and subdivision of the orbicularis oris muscle into peripheral and marginal portions (Le Gros Clark, 1924b, 1926a; Lightoller, 1934).

Muscles of the Abdominal Wall

A tupaiid feature of the abdominal wall musculature that is considered primitive, and not shared with Prosimii, is the presence of a pyramidalis muscle (Carlsson, 1922).

Tupaiids share the following features of abdominal wall musculature with Lemuroidea:

1. External oblique muscle fibers continue over the rectus abdominis muscle almost to the linea alba in _Tupaia_. In Lemuridae (especially _Cheirogaleus_) and in _Nycticebus_ muscle fibers spread over the rectus abdominis muscle to a varying extent. In Lipotyphla, however, the aponeurosis is broad (Carlsson, 1922).
2. The rectus sheath of _Tupaia_ and _Ptilocercus_ shares a structure with Madagascan lemuroids that is found in no other mammals except _Otaria_ (sea lion). The aponeurosis of the tupaiid internal oblique muscle lies dorsal to the rectus abdominis muscle in its cranial portion; in its caudal portion, however, the internal oblique aponeurosis lies ventral to rectus abdominis (Kaudern, 1910; Carlsson, 1922; Le Gros

Clark, 1924b, 1926a). This peculiarity is most strongly marked in *Tupaia*, is somewhat less evident in Lemuridae (*Lemur*, *Cheirogaleus*, *Propithecus*), and is absent in Lorisiformes and higher Primates (Kaudern, 1910; Carlsson, 1922; Le Gros Clark, 1924b). Kaudern (1910) believed this to be a very ancient feature. Carlsson (1922) observed that the internal oblique aponeurosis lies ventral to the rectus abdominis muscle in all Insectivora except Talpinae, in which it lies dorsal to that muscle.

Muscles of the Anterior Extremities

Probable primitive features of the musculature of the anterior extremities of Tupaiidae include the following:

1. The tendon of insertion of the extensor carpi radialis muscle splits into two parts as it crosses the abductor pollicis longus tendon in *Tupaia* species, in *Erinaceus* (Carlsson, 1922), and in *Suncus* (Sharma, 1958). The larger tendon attaches to the third, and the smaller to the second, metacarpal bone. In *Rhynchocyon* (elephant shrew), the single tendon attaches only to the third matacarpal bone. The muscle is completely divided into two in *Didelphis* (opossum), *Sciurus* (squirrel), Lemuroidea, and most higher Primates (Carlsson, 1922).
2. Musculus abductor pollicis brevis has but one head

in *Tupaia* species, *Erinaceus*, *Tenrec*, *Macroscelides* (elephant shrew) (Carlsson, 1922), and *Suncus* (Sharma, 1958). It arises by two heads in Lemuroidea (Carlsson, 1922).

3. Musculus opponens pollicis has not differentiated in *Tupaia*, *Sciurus*, *Didelphis*, or *Erinaceus*. While remaining inconstant in Prosimii, the muscle is present in *Callithrix* (marmoset) (Carlsson, 1922).

4. Musculus opponens digiti minimi is undifferentiated in *Tupaia*, in Lipotyphla (e.g., *Tenrec*), and in *Sciurus*. This muscle is usually developed in *Didelphis*, Lemuroidea, and *Callithrix* (Carlsson, 1922).

5. Of the deep digital extensor muscles, extensor pollicis longus and extensor indicis proprius together form one muscle, as in Erinaceidae (also in *Suncus*, according to Sharma, 1958), many other mammalian orders, and the South American monkeys. The Old World Primates, at least *Lemur* among Lemuroidea, differ. In *Didelphis*, also, both muscles appear. In *Sciurus* and Macroscelididae, the extensor pollicis longus muscle is absent (Carlsson, 1922).

Other primitive features of tupaiid forelimb musculature shared with lemuroids include the following:

1. A brachioradialis muscle is completely absent in

Ptilocercus. In this, it resembles most Lipotyphla and differs from *Tupaia*, in which this muscle is present, at least in *Tupaia minor* and *Tupaia ferruginea*. Normally, it is also found in lemurs and other Prosimii. It is possible that the brachioradialis muscle has disappeared in *Ptilocercus*; or, if the muscle has not yet differentiated from the extensor carpi radialis mass (prominently developed in this genus), the absence may be primitive (Le Gros Clark, 1924b, 1926a).

2. In *Tupaia* species, the extensor digitorum communis and extensor digitorum lateralis muscles arise by a common head that quickly divides into a stronger radial extensor digitorum communis and a weaker ulnar extensor digitorum lateralis. In the proximal half of the forearm, the tendon of extensor digitorum communis splits into four parts, continuing on to the second through fifth digits. The relatively longer tendon of extensor digitorum lateralis splits into two parts, leading to the two ulnar fingers. Both *Rhynchocyon* and *Callithrix* lack a tendon to the fifth digit. The two tendons are present in *Didelphis*, *Erinaceus*, *Petrodromus*, *Macroscelides*, *Sciurus*, and Prosimii (Carlsson, 1922), as well as in the soricid, *Suncus* (Sharma, 1958).

3. The three contrahentes muscles are attached to

the first, second, and fifth fingers in *Tupaia*, as also in *Didelphis*, Tenrecidae (Madagascan insectivores), Macroscelididae, and Lemuroidea. None are usually retained in *Erinaceus* (Carlsson, 1922) or in *Suncus* (Sharma, 1958). Primitively, in urodeles and *Emys* (Tertiary marsh-dwelling turtles), the contrahentes muscles attach to all five fingers. Their reduction in *Tupaia* is thus less than in *Sciurus*, with only contrahens V remaining (Carlsson, 1922).

4. The omohyoid muscle of *Tupaia* shows a distinct intersection, as in Primates and Chiroptera. This muscle is apparently absent in many lipotyphlous Insectivora (Årnbäck-Christie-Linde, 1907; Le Gros Clark, 1924b; Gaughran, 1954; Sharma, 1958). In *Blarina*, however, Gaughran (1954) found a thin, strap-like omohyoid muscle, without tendinous intersection.

5. *Tupaia* species have four lumbricales muscles, as do *Didelphis*, *Gymnura*, *Macroscelides*, and Lemuroidea, as well as *Sciurus*. In *Erinaceus*, the number is variable or the muscles may be completely absent (Carlsson, 1922).

6. Since dorsal interosseous muscles are found in urodeles, *Trichosurus* (common phalanger or Australian "opossum"), and *Didelphis* (common Virginia opossum), as well as several other marsupials, they are regarded

as primitive muscles. While clearly apparent in Tupaia, Lemuroidea, and Callithrix, they are not observable in Sciurus (Carlsson, 1922).

7. Lower mammals have musculi flexores breves profundi for each finger. The full primitive complement persists in Tupaia, as well as in Didelphis, Erinaceus, Prosimii, and Callithrix (Carlsson, 1922), and also in Suncus (Sharma, 1958). Sciurus shows some reduction in having these muscles only for the four ulnar fingers (Carlsson, 1922).

8. Musculus flexor pollicis brevis sublimis is present in Tupaiidae, Didelphis, Tenrec, and Lemuroidea (Carlsson, 1922; Le Gros Clark, 1924b, 1926a). It is absent from Erinaceus, Sciurus (Carlsson, 1922), and Suncus (Sharma, 1958).

Prosimii have a far more advanced differentiation of the hand muscles generally than is attained in Tupaia.

Tupaiids and lemuroids share a few features that probably represent advances. These include the following:

1. The coracobrachialis muscle is normally fully developed in tupaiids and lemurs, but frequently is lacking (wholly or in part) among Insectivora (Davis, 1938).

Sharma (1958) did not find this muscle in

Suncus, and noted that it has not been reported for any soricoid genus. Musculus coracobrachialis, however, is present in the talpid, *Uropsilus*, which is regarded as primitive.

2. In *Tupaia*, the dorso-epitrochlearis muscle is completely duplicated. Two heads of origin are found in *Dendrogale* (smooth-tailed tree shrew) and in lemurs. This similarity is probably due to locomotor patterns for climbing. Although double here, many animals more arboreal than tree shrews and lemurs have a simple dorso-epitrochlearis muscle, as do many cursorial animals. The single head unites with the triceps brachii muscle in insectivores such as Erinaceidae, Macroscelididae, and *Suncus* (Soricidae) (Carlsson, 1922; Le Gros Clark, 1924b; Davis, 1938; Sharma, 1958).

3. In *Tupaia* and *Dendrogale*, as in *Lemur* and other Prosimii, the lateral head of the triceps brachii muscle is double, having both superficial and deep parts. Only the upper part (arising from the neck of the humerus) apparently is represented in lipotyphlous insectivores and sciuromorph rodents (Le Gros Clark, 1924b; Davis, 1938; Sharma, 1958).

4. It has been observed that both the first and fifth digits of *Tupaia* can diverge widely. Musculi contrahentes II and V here arise from a common median raphe.

Musculus contrahens I is independent of this raphe, to form a small muscle controlling pollex alone. (A similar pattern is found in the foot.) This feature has been interpreted by Le Gros Clark (1926a, 1927) and Napier (1961) as indicative of close affinity between Tupaiidae and Lemuriformes. To Haines (1958), however, this similarity between _Tupaia_ and _Lemur_ arose by convergence for arboreal locomotion. In _Tupaia_ the main raphe lies between contrahentes II and V, with a smaller one occurring between I and II. In _Lemur_, however, the major raphe lies between contrahentes I and IV. The major raphe, providing some functional opposability, thus shows differing anatomical development in these two groups. _Tupaia_ also shows a far more specialized arrangement of its hypothenar muscles (for opposition of radial digits to hypothenar pad) than does _Lemur_ (Haines, 1958).

5. Some muscle fibers called "_Carpalballenmuskeln_" (muscles of the carpal pads) are found in both carpal pads of _Tupaia_ species. Such have not been described for lipotyphlous insectivores. An ulnar _Carpalballenmuskel_ is differentiated in _Sciurus_. Lemuroids have both the ulnar and radial muscles developed. Such muscle fibers are absent in _Didelphis_ on the one hand, and in _Callithrix_ on the other (Carlsson, 1922).

Muscles of the Posterior Extremities

Muscles of the lower extremities show similar trends, thus demonstrating greater similarity of Tupaiidae to Lemuroidea than to most Insectivora. Among the similarities to Lemuroidea are the following:

1. The elements of the iliopsoas muscle are fully differentiated at their insertion in *Tupaia* and *Ptilocercus* (Le Gros Clark, 1924b, 1926a). The form and disposition of the iliacus muscle in *Tupaia* and *Galago* are identical; it is similarly disposed in *Tarsius* (Carlsson, 1922; Le Gros Clark, 1924b). Davis (1938) found the iliacus muscle of *Dendrogale* to be quite similar to that of *Tupaia*, with the usual lateral and medial heads.
2. A distinct pyriformis muscle is present in *Ptilocercus*, *Tupaia*, and *Dendrogale*, as well as in Macroscelididae and Prosimii, but absent in all Lipotyphla (Le Gros Clark, 1924b, 1926a; Davis, 1938; Sharma, 1958).
3. Davis (1938) described the gluteus medius and gluteus minimus muscles as quite readily separable in *Dendrogale*, with gluteus medius being bilaminar. Carlsson (1922) found gluteus medius superior to be a relatively more independent muscle in *Tupaia*, Macroscelididae, and Lemuridae than in Lipotyphla.

4. Musculus sartorius is normally present in tupaiids and lemurs but lacking in lipotyphlous insectivores except *Erinaceus* (Le Gros Clark, 1924b, 1926a; Sharma, 1958).

5. The extent of the tibial attachment of the popliteus muscle in *Ptilocercus* agrees with *Tupaia*. This is considered to be a lemuroid feature since the muscle does not extend downward beyond the upper fifth of the tibial shaft. Other groups display greater length: *Didelphis* and *Suncus*, one-third; *Erinaceus*, one-half; *Callithrix*, one-fourth (Carlsson, 1922; Le Gros Clark, 1924b, 1926a; Sharma, 1958).

6. Musculus plantaris in *Tupaia* is united with the lateral head of the gastrocnemius muscle, as in Lemuridae, but not as in *Erinaceus* (Carlsson, 1922).

7. Musculus flexor brevis digitorum in *Tupaia* resembles Lemuroidea but is unlike Lipotyphla and *Sciurus* in having two heads of origin from the deep flexor tendons and the plantar fascia. In having the muscle attached directly to os calcis, *Tupaia* parallels only Primates and some Chiroptera (Carlsson, 1922).

8. Musculus crureus frequently is absent among Lipotyphla, although found in *Tupaia* and Lemuroidea (Le Gros Clark, 1924b).

9. Occasionally, *Tupaia* shows a distinct musculus

subcrureus. Its presence is normal in Prosimii. It is completely absent in Lipotyphla (Le Gros Clark, 1924b).

10. *Tupaia*, with three musculi contrahentes, shows less reduction of this muscle group than any insectivore. *Tarsius* and *Lemur* retain musculi contrahentes for all five toes (Carlsson, 1922).

11. Musculus abductor hallucis is well developed in *Tupaia* and Prosimii. It is absent in Insectivora, according to Le Gros Clark (1924b). Sharma (1958) found a long, slim musculus abductor hallucis in *Suncus murinus*.

12. Musculus peroneus digiti quarti is differentiated in *Tupaia* and lemurs but not in insectivores, according to Le Gros Clark (1924b). This muscle is present, however, in *Suncus murinus* (Sharma, 1958).

13. Musculus peroneus quinti and musculus quinti digiti, in being differentiated into parts, shows similarity between *Tupaia* and Lemuroidea (Le Gros Clark, 1924b; Sharma, 1958).

Primitive features of the musculature of the posterior extremities include the following:

1. A tensor fasciae femoris muscle is undifferentiated (from gluteus maximus) in both *Ptilocercus* and *Tupaia*, although Le Gros Clark cites Leche as having found it in *Tupaia* ferruginea (Le Gros Clark,

1924b, 1926a). It is of interest that this muscle is differentiated in *Suncus* (Sharma, 1958).

2. The tenuissimus muscle is present in *Ptilocercus* and *Tupaia*; it is generally present in Lipotyphla but absent in Lemuroidea. Since this muscle represents the femoral head of musculus biceps femoris of higher Primates, it is clearly a primitive feature (Le Gros Clark, 1924b, 1926a; Sharma, 1958).

3. Musculus extensor digitorum communis longus of *Ptilocercus* and *Tupaia* is evidently primitive in its origin from the femur (lateral condyle). Lipotyphla and *Sciurus* also retain a femoral origin. In Lemuroidea, the origin has shifted (presumably secondarily) to the tibia and fibula. *Didelphis* shows a somewhat parallel secondary shift to the head of the fibula (Carlsson, 1922; Le Gros Clark, 1924b, 1926a; Sharma, 1958).

Circulatory System

Serology

J. Buettner-Janusch and V. Buettner-Janusch (1964) have reported an electrophoretic study of cell hemolysates from different primates and insectivores. One can thereby differentiate certain taxa above generic levels. Hemoglobin of *Tupaia glis* has one component that moves more slowly than hemoglobin of any primate studied. It does not resemble the hemoglobin of any insectivores studied. *Rhynchocyon chrysopygus*, an elephant shrew, has two very fast-moving components, resembling the hemoglobin of *Perodicticus potto*. A feature common to adult prosimians and elephant shrews is the relatively high level of alkali-resistant hemoglobin. In Anthropoidea, only fetal blood contains alkali-resistant hemoglobin.

In 1963, Maisel and Goodman reported an immunoelectrophoretic study of proteins in primate lenses. Precipitin bands decrease with phylogenetic distance from the homologous species; thus bands decrease as one proceeds from Old World monkeys, to hominoids, to New World monkeys, to prosimians (including tree shrew), to non-primates. No reaction occurs with a great variety of non-primate mammals. This would tend to confirm primate affinity for the tree shrew. There was no indication that insectivores were included in the study.

In the immunochemical study made by Hafleigh and Williams (1966), relative cross-reactivity was determined by the quantitative precipitation reaction. Serum albumins were tested against human serum albumin. The immunochemical correspondence value for *Tupaia glis* (31 per cent) is well within the range of Prosimii, being a few curve area percentage points

lower than for *Lemur* species (34-37 per cent), but similar or a few points higher (closer to human) for *Perodicticus potto* (31 per cent), *Galago crassicaudatus* (28 per cent), and *Propithecus verrauxi* (22 per cent). The only insectivore tested was *Erinaceus* (17 per cent), with a correspondence several points below that of any prosimian, although in a range expected for a near relative of primates. (Pig shows 8 per cent correspondence.)

If the isoimmunization theory of evolutionary arrest (Goodman, 1963) is correct, the high cross-reaction of the tree shrew albumin might not be an accurate indication of degree of relationship. The correspondence to other prosimians might be a coincidence. Further qualitative and quantitative analysis of prosimian and insectivore albumins is necessary to clarify the nature of the relationship. Goodman's (1964) report indicates that lorisids are closer to lemurids than to either tupaiids or anthropoids. With respect to serum proteins at least, lemurid genes have evidently shown more rapid divergence from the ancestral or basal primate type than have the homologous genes in tupaiids and lorisids.

In his 1962 report of similar results, Goodman indicated that some serum protein types evolve more rapidly than others. Albumins apparently change slowly, showing marked divergence in Primates, only as the lemurid-lorisid-tupaiid level is reached; gamma globulins, however, have evolved much more rapidly. Albumin is synthesized early in fetal life; gamma globulins, late.

In cross-reactions of antisera to human serum proteins (Goodman, 1963), tupaiid serum globulins show greater resemblance to those of hedgehog than to those of primates; yet tupaiid serum albumins resemble those of primates more closely. Human albumin corresponds more closely with tree shrew albumin than with lemur albumin. Goodman (1963) postulated that albumin evolution would have been more rapid in lemur (with epitheliochorial placenta) than in tupaiids (with endotheliochorial placenta) and human females (with hemochorial placenta). In the latter two situations, maternal isoimmunizations would have caused retention of very primitive genetic patterns. Since serum globulins develop at a later ontogenetic stage, they would not have been so much affected, even though hedgehog also possesses a hemochorial placenta.

Based on production of chicken antisera to the serum of prosimians and insectivores, Goodman (1963) postulated a kind of phylogeny. Although there are antigenic differences between lorisids

(Galago, Loris, Perodicticus) and lemurids (Lemur), each family resembles the other more closely than either resembles tupaiids or anthropoids. It may be concluded that Lorisiformes and Lemuriformes did not separate until after their common ancestor had separated from antecedents of Anthropoidea. There appears to be no special relationship between Tupaioidea and Lemuroidea. Using anti-hedgehog and anti-tree-shrew sera, Goodman (1963) found closer correspondence between hedgehog and tree shrew than either shows to other mammals tested (kangaroo, galago, lemur, man, rat, rabbit, dog, elephant, horse, cow); yet the tree shrew-hedgehog affinity is not at all close since the heterologous cross-reaction, in each case, was far less than the homologous one. Thus, Tupaioidea may well have separated from other mammals during the initial major eutherian radiation of the late Cretaceous period.

Goodman (1962) used two-dimensional starch-gel electrophoresis to separate macromolecular complexes within serum. These separations show constellations of components forming patterns that are distinctive for taxonomic groups. Tree shrew (Tupaia glis) and hedgehog (Erinaceus) have very different patterns.

Johnson and Wicks (1962), using

electropherograms to characterize serum proteins, found each species has a qualitatively and quantitatively distinct pattern. In some orders the albumin migrates farther than in the human control; in others, less far. In Didelphidae (Marsupialia), albumin migrates at a rate which is 90 per cent of that of the human control. The rate in Soricidae (shrews) is about the same as in man, while the albumin moves slightly faster in Talpidae (moles). Cercopithecidae (Old World monkeys) are more similar to Hominidae than are Tupaiidae; the latter differ no more from Hominidae than one family does from another within other orders.

An electrophoretic study by Lange and Schmitt (1963) showed that *Tupaia glis* has no recognizable prealbumins. Prealbumins are also lacking in *Cebus* and *Ateles* and are weak in *Cacajao*--all New-World genera. *Lemur* has but one prealbumin; Pongidae and most Cercopithecidae have two. *Tupaia* shows an especially short gamma-globulin zone, one shorter than any primate tested. A uniform, haptoglobin 1-1 phenotype is found in *Tupaia*, as in all Primates observed. In contrast, the transferrin system displays great polymorphism among Primates. *Tupaia* shares the A_5 transferrin with *Presbytis* and *Lemur*, and shares the B_O transferrin with Europide

Homo, *Symphalangus*, *Macaca*, *Papio*, and *Presbytis*.

Layton (1965) pointed out that human atopic reagins (serum antibodies responsible for hypersensitivity of mucous membranes, as in hay fever) can be used to sensitize (passively) other Primates. He was able to induce passive allergy in a variety of monkeys and prosimians but not in *Tupaia glis* or in any of a variety of non-primates, including opossum and bat but no insectivores.

Circulatory Organs

Starck (1960) noted that the spleen displays different gross forms showing evolutionary trends. The elongate, ribbon-like form observable in Tupaiidae may be regarded as the ancestral primate (also mammalian?) model. This form is found in many Prosimii and in Insectivora; however, among prosimians, a number of specializations appear.

Frick's (1960) description of the heart of *Tupaia glis* indicated that it shares in the variability of prosimians in several features. Without comparable descriptions of insectivore hearts, little can be said regarding phylogeny. Le Gros Clark (1926a) stated that the heart shows the "generalized mammalian condition." In support of this is the observation (based on Frick's illustrations) that base-apex length exceeds base diameter considerably, and that the heart axis deviates but little from the long axis of the thorax. Hill (1953b) noted that the following are usually absent in lower mammals: coronary (Thebesian) valves, caval (Eustachian) valves, fossa ovalis, and annulus ovalis. In *Tupaia*, Frick (1960) found that fossa and annulus ovalis are both present; the caval valves are present, but share in the variability usual among strepsirhines; typical coronary valves are lacking.

In connection with the system of blood vessels, few phylogenetic trends can be indicated due to lack of adequate data (Davies, 1948).

Le Gros Clark (1926a) noted that the absence of a common iliac artery in *Ptilocercus* may be regarded as primitive. Such a common vessel is usually present in strepsirhines (Hill, 1953b).

Ptilocercus shares with *Lemur catta* the arrangement of arteries in the arm (brachium), where the brachial artery is relatively small and the principal vessel is the superficial brachial artery (Le Gros Clark, 1926a).

The presence of paired precavae, as in *Tupaia* and *Ptilocercus*, is characteristic of primitive mammals (Le Gros Clark, 1926a).

Ptilocercus has a single (left) azygos vein. This is found in many marsupials, including Phalangeridae. (A left vena azygos is also found in certain rodents and artiodactyls.) (Le Gros Clark, 1926a)

Except for description of the mode of branching of the arch of the aorta and the relations of the internal carotid system in the middle ear cavity and walls, little information has been published on cranial arteries of Ptilocercus (Le Gros Clark, 1926a), and virtually no information is to be found for Tupaia or Dendrogale species. The observations of phylogenetic interest will be noted in the discussion of results of the present study.

MATERIAL AND METHODS

For the study of the carotid vessels, four mature individuals (three males and one female) of the Malayan tree shrew, Tupaia glis Diard, were used.

The first three tree shrews (numbered: 1, 2, and 3) were embalmed after death. The preserving fluid used was a standard mixture of potassium nitrate, borax, boric acid, thymol, menthol, salicylic acid, oil of wintergreen, ethylene glycol, formalin, and water. Then the arterial system was perfused with acetone to flush out the blood. The arterial systems of these three tree shrews were subsequently injected with red latex. Additional tree shrews injected in this manner did not display adequate penetration of latex into the arteries of the cranial region. This was probably due to contraction of vessels by embalming fluid or acetone. Only the three animals described here were adequately injected for observation.

The fourth tree shrew (number 4) was therefore injected with a more finely dispersed silicone rubber compound called Microfil.[1] Another preliminary procedure substituted in the case of tree shrew 4 included perfusion with Ringer's warm-blooded saline solution containing heparin. Penetration of finer vessels was greatly improved by use of these procedures.

Tree shrew 1 had been purchased as a dead specimen; thus cause and time of death were unknown. Animals numbered 2, 3, and 4 were obtained in the living state. Perfusion, for flushing out of blood and for embalming, was carried out while the animals were anaesthetized by ether. Injection of the colored latex was carried out after intervals of twelve to twenty-four hours. Microfil was injected immediately after perfusion, within fifteen minutes after death, in tree shrew 4.

Observations have been limited to the gross anatomy of the carotid vessels. Due to the small size of the animal, most dissection required the use of micro-dissecting instruments and a Zeiss binocular dissecting microscope.

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[1] Microfil is the trademark of the Canton Bio-Medical Products Company, Swarthmore, Pennsylvania.

DESCRIPTIVE ANATOMY

The branching pattern and distribution of the carotid system will be described in the following order: arch of aorta, common carotid artery, external carotid artery, internal carotid artery. Description of the stapedial branch of the internal carotid artery precedes that of the arteries at the base of the brain, which include the vertebro-basilar and cerebral carotid groups.

The Arch of the Aorta

The mode of origin of the major branches of the arch of the aorta shows minor variation in the four tree shrews observed. In three out of four individuals, there are two main trunks: (1) a long truncus brachiocephalicus dexter and (2) a very short (about one millimeter in length) truncus brachiocephalicus sinister. In one case, when the common areolar connective tissue sheath around the left common carotid and left subclavian arteries was cleared away, the left brachiocephalic trunk was found to be only a fraction of a millimeter in length. In the fourth individual, three main trunks arise from the arcus aortae:

(1) truncus brachiocephalicus, (2) arteria carotis communis sinistra, and (3) arteria subclavia sinistra. These arise in order from right to left, with the second and third lying close together.

The (right) brachiocephalic trunk divides into the arteria subclavia dextra and the arteria carotis communis dextra. The division occurs at the level of the sternoclavicular joint, at the right lateral margin of the trachea, the brachiocephalic trunk having crossed the trachea obliquely.

The Common Carotid Artery

There is only one collateral branch of the left common carotid artery: the arteria thyroidea inferior, which is given off about five to six millimeters above the origin of the left common carotid artery, also receives a contribution from the (right) brachiocephalic artery. The brachiocephalic contribution was not observed in two cases.

Each common carotid artery ends at a level deep to, or just caudal to, the posterior belly of the digastric muscle. The hypoglossal nerve crosses just lateral to the carotid bifurcation. The latter division results in formation of the arteria carotis externa and arteria carotis interna. The arteria carotis externa is detectably larger in calibre than the arteria carotis interna in all but one case: in tree shrew 2, they are approximately equal. The difference is always slight. These two diverging vessels continue their course, with the vagus nerve, deep to the posterior belly of the digastric muscle.

The External Carotid Artery

Although the external carotid artery is not of primary interest here, certain general features must be described to demonstrate its relations with the internal carotid system.

Within one millimeter of its origin (except on the right side of tree shrew 3), the arteria carotis externa sends off the arteria occipitalis. Arising within the V-shaped carotid bifurcation, this branch parallels the course of the arteria carotis interna to reach the muscles supplied. On the right side in tree shrew 3, the occipital artery originates, at a considerably higher level, from a common trunk with the posterior auricular artery and the major branch of supply to the parotid gland. This common trunk lies inferolateral to the auricle, deep to the parotid gland, and caudal to the masseter muscle.

In all cases, the arteria thyroidea superior is given off by the arteria carotis externa within one to three millimeters beyond the carotid bifurcation.

The hypoglossal nerve crosses at, or just beyond, this level. The superior thyroid artery curves mediad and then runs rather straight caudally to reach the thyroid gland and the larynx.

The next major division of the arteria carotis externa (two to five millimeters farther on), in three animals, is a bifurcation into a more superficial branch that courses ventrolaterad as the arteria lingualis and a deeper branch that courses dorsolaterad as the continuation of the arteria carotis externa. The latter is usually somewhat larger than the arteria lingualis; they may be almost equal in caliber.

The arteria lingualis stem very quickly sends off a large and rather superficial arteria submandibularis to supply the submandibular and sublingual glands. The main continuation of the arteria lingualis remains at a deep level, coursing toward the tongue.

Tree shrew 4, however, displays a variation of this branching pattern. Here, one and one-half to two millimeters beyond the origin of the superior thyroid artery, the external carotid artery sends a large, independent submandibular artery to the submandibular and sublingual salivary glands. About two millimeters further on, after a sharp dorsal turn, the external carotid artery gives off a common trunk (about equal in calibre to the external carotid continuation) for the arteria lingualis and arteria facialis. The common trunk courses rostrally for about six millimeters, sending off muscular twigs to the masseter and digastric muscles and some supplemental twigs to the submandibular and sublingual salivary glands. The facial artery appears to be the continuation of the common trunk.

In tree shrews 1, 2, and 3, however, the arteria carotis externa continues for about three to six millimeters beyond the exit of arteria lingualis before sending off the rather small arteria facialis deep to the posteroventral margin of the masseter muscle.

Whatever its mode of origin, the slender facial artery continues along the typical rostral course deep to the lower border of the masseter muscle. _En route_, it sends off muscular branches and then turns dorsally to cross the mandible near the cephalic border of the masseter muscle. In tree shrew 4, one could observe the very rich vascular supply to the vibrissal area of the snout; however, these branches appeared to arise mainly from the infraorbital artery.

In all cases, the external carotid artery takes a sharp dorsal turn after exit of the lingual artery and here lies deep to the parotid salivary gland. Caudal to the temporomandibular joint, it ends by breaking up into a series of branches. Whereas the major one does continue the stem as the arteria maxillaris, it is not at all evident that the arteria temporalis superficialis is the other major terminal branch. The superficial temporal artery is not a conspicuous vessel in this species.

This area of terminal ramification of the arteria carotis externa appears to be quite variable. A common pattern shows the major branch of supply to the parotid gland, the ramus parotideus, arising from the arteria carotis externa very close to the arteria auricularis posterior (in two animals bilaterally, and in one animal unilaterally). There may be a common stem for the ramus parotideus and the arteria auricularis posterior (in one animal bilaterally, in one animal unilaterally). As mentioned previously, the right side of tree shrew 3 shows a common stem for the ramus parotideus, arteria occipitalis, and arteria auricularis posterior. The arteria temporalis superficialis arises, typically, a short distance further along the main stem, which may now be designated as the arteria maxillaris.

The External Carotid Artery (Maxillary Division)

The maxillary artery continues rostrad, ventral to the pinna, and then markedly mediad as it crosses the anterolateral wall of the tympanic bulla. As it courses deep to the dorsal part of the masseter muscle, it sends twigs to that muscle, to the pterygoid muscles, and to the parotid gland. As the arteria maxillaris reaches the line of junction between the cranial wall and the dorsal bulla wall, deep to the lateral pterygoid muscle, it gives off a slender ramus anastomoticus cum arteria stapedia, which may be regarded as the proximal portion of the ramus inferior arteriae stapediae. (See Figure 1.) This anastomotic branch, relative to the arteria maxillaris, courses posterodorsally and passes through an opening lying just anterodorsal to the inner end of the external acoustic meatus to join the stem of the arteria stapedia. The latter lies within the dura mater, having just emerged from its canal in the medial wall of the tympanic cavity. This is also approximately the level at which the stapedial artery (superior ramus) gives off a large meningeal branch coursing dorsally along the line of the fissure between cerebrum and cerebellum. On one side in one individual there appear to be two diverging branches of the common anastomotic trunk penetrating

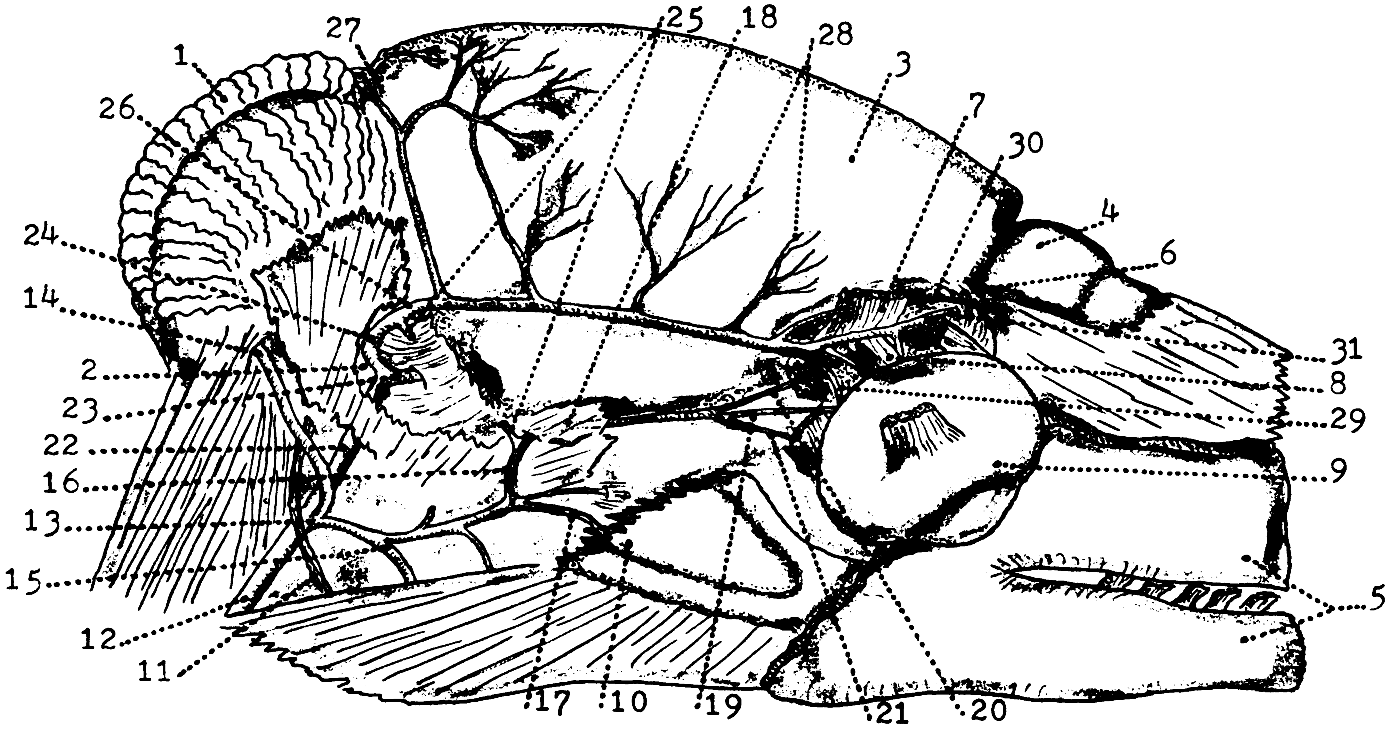


Figure 1. Lateral View of the Cranial Region.

Key to numbers used: 1, cerebellum; 2, medial wall of tympanic bulla; 3, cerebrum; 4, olfactory lobe; 5, skin of snout; 6, wall of orbit; 7, superior rectus muscle; 8, optic nerve; 9, eyeball; 10, mandible; 11, hypoglossal nerve; 12, common carotid artery; 13, external carotid artery (stem); 14, occipital artery; 15, lingual artery; 16, (internal) maxillary artery; 17, inferior alveolar artery; 18, maxillary artery passing through the external alisphenoid canal; 19, infraorbital artery; 20, orbital ramus of infraorbital artery; 21, superior alveolar artery; 22, internal carotid artery (stem); 23, cerebral carotid (promontory) artery; 24, stapedial artery (stem); 25, inferior ramus of stapedial artery; 26, superior ramus of stapedial artery; 27, middle meningeal artery; 28, accessory meningeal arteries; 29, lacrimal artery; 30, frontal artery; 31, ethmoidal artery.

the skull wall separately. Only one of these branches joins the stapedial artery as the latter emerges from the middle ear region. On one side in another individual the anastomotic branch joins the stapedial artery farther posteriorly by piercing the anterior bulla wall. Near the maxillary end, this anastomotic branch has collateral twigs supplying the bulla wall itself. The connection with the maxillary artery was not observable in this case nor on one side of another individual. The connection may or may not have been present in these two instances. Connection with the arteria stapedia was demonstrable in all cases. Collateral branches to the bulla wall were commonly seen.

In the region medial to the mandible and rostral to the temporomandibular joint, the arteria maxillaris gives off the large arteria alveolaris inferior that enters the mandibular foramen almost immediately, lying directly ventral to the inferior alveolar nerve.

As the arteria maxillaris itself continues its rostromedial course, it sends off a series of branches to pterygoid and temporal muscles. In one case there is a major muscle branch with several collateral twigs.

As the arteria maxillaris approaches the skull base, it enters the external alisphenoid canal in the small, laterally projecting external alisphenoid process. (See Figure 1.) After its brief passage through this canal (no branch being detectible within the canal), the arteria maxillaris again appears briefly in the infratemporal region before entering the orbit to cross its floor, accompanying, and lying immediately lateral to, the large maxillary division of the trigeminal nerve.

The External Carotid Artery (Infraorbital Division)

From the afore-mentioned juncture, the arteria maxillaris may be called the arteria infraorbitalis. This portion sends branches to the palate. The artery also sends off a major branch, the arteria alveolaris superior, which accompanies a comparable nerve branch.

A large medial branch of the arteria infraorbitalis extends across the orbital floor to the ethmoidal foramen in the ventromedial orbital wall. Before entering the cranial cavity (in the region of the olfactory lobe), this anastomotic ramus orbitalis of arteria infraorbitalis joins the ethmoidal branch of the stapedial artery (superior ramus), to be described later. This anastomosis was observed only in tree shrews 3 and 4, bilaterally. (Unfortunately, it could not be demonstrated with certainty in tree shrews 1 and 2, due to the earlier method of dissection used. Here it was largely or completely destroyed, presumably.) Ramus orbitalis, in tree shrew 4, could be seen to send off a few small branches to inferior ocular muscles.

The infraorbital artery leaves the orbit, by way of the infraorbital canal and foramen, to enter subcutaneous areas of the snout region.

The Internal Carotid Artery
(Stem and Major Branches)

The arteria carotis interna ascends obliquely cephalodorsad from its origin deep to, or below, the caudal border of the posterior belly of the digastric muscle. After a rather straight, unbranched course to the posteromedial bulla wall, the artery passes through the carotid foramen to enter a thin-walled (translucent) bony canal in the medial wall of the tympanic cavity. For the remainder of its course through the tympanic cavity, the arteria carotis interna and its branch, the arteria stapedia, remain within such bony canals. The bifurcation occurs about four to five millimeters after entrance to the bulla. The two arteries show no appreciable size difference; if one is slightly larger, it is the arteria stapedia. The continuation of the arteria carotis interna (arteria promontorii) passes rostrally and medially to cross the convexity of the promontorium and enter the cranial cavity by passing through the foramen lacerum medium, located where alisphenoid and basisphenoid join the petrosal portion of the temporal bone. The arteria promontorii is not at all "reduced" or attenuated.

The further course of the arteria carotis interna (arteria promontorii), as the arteria carotis cerebri, will be described with the circulus arteriosus cerebri and associated arteries at the base of the brain.

The Stapedial Artery (Tympanic Portion)

As the arteria stapedia courses rostrodorsally, it passes between the crura of the stapes and thence continues its course within its bony canal in the incomplete septum separating the epitympanic sinus from the loculus. It enters the cranial cavity at the anterior margin of the os petrosum. (See Figure 1.) The cranial portion of the arteria stapedia is entirely intradural in position and in distribution. Immediately upon entering the cranial cavity, the arteria stapedia sends off the arteria meningea media that extends dorsally along the groove between the flocculus and the temporal lobe of the brain, continuing on toward the longitudinal fissure.

The Stapedial Artery--Inferior Ramus

At about the same level, the ramus inferior (anastomotic branch to the maxillary artery) arises from the stem of the stapedial artery. This branch extends through the cranial wall and courses rostroventrally along the anterior bulla wall. Although this vessel is constant in all individuals observed, it is very slender, being one-third or less of the size of the stapedial stem. It sends collateral twigs to the bulla wall.

The Stapedial Artery--Superior Ramus (Cranial Portion)

The continuation of the main stem or ramus superior of the arteria stapedia courses rostrally and somewhat ventrally, across the temporal lobe, within the dura mater. In tree shrew 1, this portion sends off one dorsally directed branch, possibly comparable with a ramus meningeus accessorius. Tree shrew 2 shows three additional, smaller, ascending dural branches of this intracranial portion of arteria stapedia (ramus superior).

The Stapedial Artery--Superior Ramus (Orbital Portion)

On arrival in the orbit, the ramus superior arteriae stapediae gives off a slender arteria lacrimalis that courses along the upper border of the posterior rectus muscle to reach the lacrimal gland. (See Figure 1.) About three millimeters deep to the conjunctival fornix, the lacrimal artery bifurcates, sending a branch to each of the separate glandular lobes.

At the same point or within one to two millimeters, the main stem of the ramus superior arteriae stapediae sends off a more substantial branch, the arteria frontalis, that remains close to the orbital roof, above the superior rectus muscle. (See Figure 1.) On reaching the dorsolateral region of the orbit, the arteria frontalis joins a branch of the maxillary division of the trigeminal nerve. The vessel and nerve continue through the supraorbital foramen to the subcutaneous tissue of the dorsolateral snout region. No collateral branches of the frontal artery could be observed within the orbit.

The main trunk (larger in calibre than the frontal artery) of the stapedial artery continues its course anteriorly between the superior rectus muscle and the retractor bulbi muscle that thinly covers the optic nerve. The vessel crosses this areolar space at a right angle with the superior rectus fibers. (See Figure 1.) Branches to extrinsic eye muscles arise from this stapedial trunk and certain of its larger branches.

As the stapedial stem nears the rostral end of the zone between the superior rectus muscle and the retractor bulbi muscle, the overall rostromedial course is continued by the slender arteria ethmoidalis that reaches the dura mater covering the olfactory lobes, by way of the ethmoidal foramen in the anteromedial orbital wall. (No anastomoses with branches of the internal carotid artery supplying the substance of the lobes themselves could be detected in this area.)

The ethmoidal artery could be seen (through the translucent orbito-cranial wall) to pass dorsally along the cephalic border of the olfactory lobe. Dissection revealed that, on reaching the dorsal surface of this lobe (within the covering dura mater), it crosses the lobe anteromedially. About one millimeter lateral to the medial border of the lobe, this dural vessel makes a sharp turn forward through the cribriform plate to enter the region of the nasal mucosa, which, in an excellent injection (tree shrew 4), is observed to contain a highly complex olfactory or ethmoidal rete of fine arteries.

It will be recalled that the infraorbital artery sends an anastomotic branch, the ramus

orbitalis, to join this ethmoidal artery as it enters the ethmoidal foramen.

In caliber, the real continuation of the stapedial artery appears to be the division that bends sharply downward and laterally toward the bulbus oculi, close against the anterior aspect of the optic nerve and deep to the anterior rectus muscle. Having given off muscular branches and additional twigs to the optic nerve sheath and sclera, this trunk terminates in branches of supply to the inferior and posterior rectus muscles. In addition to these small twigs, the arteria stapedia also sends off some larger collateral branches to be described now.

While still lying deep to the superior rectus muscle, the stapedial artery gives off a large branch coursing distally, more or less parallel with the parent trunk. This branch spends itself in sending off a long series of collateral branches to Harder's gland, as it continues deep to that gland along its considerable length. Before this branch reaches Harder's gland, however, it sends off a large collateral branch at a right angle to the trunk. This collateral branch courses ventral to the optic nerve, just deep to the inferior rectus muscle, supplying extrinsic muscles of this inferior region.

At the anterior border of the superior rectus muscle, the stapedial artery sends off a very short common trunk from its lateral surface; the common trunk, in turn, gives rise to four branches. These supply extrinsic muscles, including superior rectus, superior oblique, anterior rectus, and retractor bulbi muscle slips.

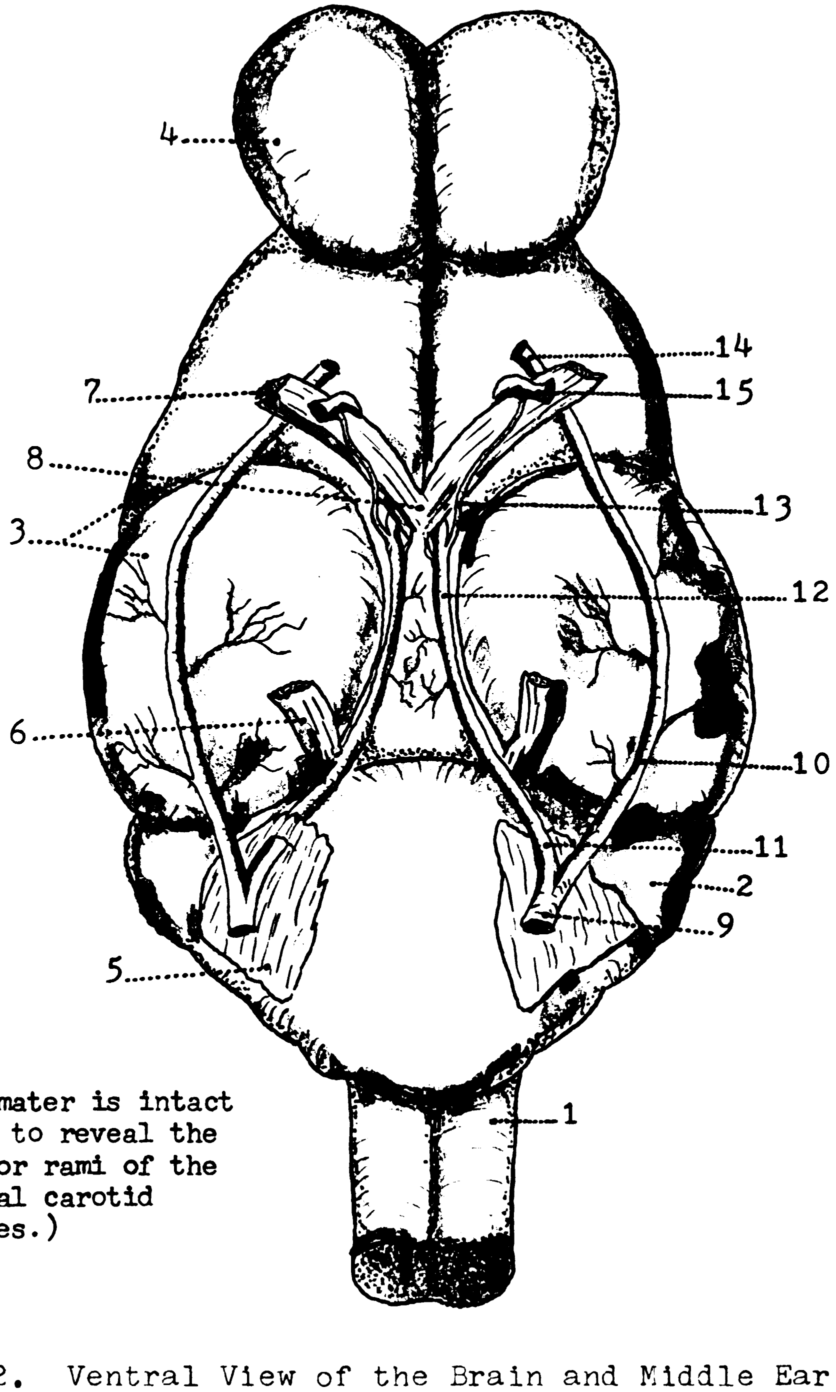
Another series of collateral branches of the stapedial trunk constitute the arteriae ciliares. These spring from a collateral branch that serves as their common trunk of origin. These branches tend to be prolonged downward along the optic nerve and onto the bulb in a brush-like formation. On reaching the bulb, further branching of this more or less parallel type occurs; thus there are (in tree shrew 4) three major branches and three to four lesser branches of this ciliary artery group. Many of them course within the sheath of the bulbus oculi to reach the region just deep, and proximal, to the insertion of the retractor bulbi muscle slips. Although some finer branches penetrate the bulb _en route_, the major branches penetrate the sclera in the terminal region indicated above. A large proximal branch of the ciliary common trunk crosses the ventral surface of the optic nerve obliquely, to reach the

ventrocaudal and dorsocaudal aspects of the nerve and bulb.

The arteria ophthalmica (branching from the intracranial arteria carotis interna) anastomoses with the branch of the arteria stapedia that serves as the common trunk for the ciliary branches; thus the exceedingly small ophthalmic artery is functionally in a position to supply blood only to the ciliary arteries. (See Figure 2.) It supplies no other structures within the orbit. The arteria ophthalmica was very difficult to locate and trace in all individuals except tree shrew 4. In tree shrew 3, it could not be found on the right side. In tree shrew 1, it could not be traced beyond the optic nerve. Failure to be injected with latex could make it all but impossible to find, even with a binocular microscope. Normally, its path may be traced across the ventrolateral surface of the optic chiasma and thence obliquely across the ventral surface of optic nerve to the ciliary trunk lying at the anterior margin of that nerve.

The Arteries at the Base of the Brain

In describing the arteries at the base of the brain, the posterior vertebro-basilar group will be taken up first, to be followed by the internal carotid group at more anterior levels. The two groups



(Dura mater is intact
except to reveal the
anterior rami of the
cerebral carotid
arteries.)

Figure 2. Ventral View of the Brain and Middle Ear.

Key to numbers used: 1, medulla oblongata; 2, cerebellum; 3, cerebrum; 4, olfactory lobe; 5, dorsomedial wall of tympanic bulla (remnant); 6, trigeminal nerve; 7, optic nerve; 8, optic chiasma; 9, internal carotid artery (stem); 10, superior ramus of stapedial artery; 11, cerebral carotid (promontory) artery; 12, anterior ramus of cerebral carotid artery; 13, ophthalmic artery; 14, ethmoidal artery; 15, ciliary artery (stem).

are joined at the transition from rhombencephalon to mesencephalon levels.

The Vertebral Artery

The arteriae vertebrales curve around the lateral surfaces of the caudal medulla oblongata, extending obliquely cephalad as they pass from the dorsolateral to the mid-ventral surface.

Each arteria vertebralis, as it extends obliquely cephalad toward the arteria basilaris, gives off three branches from its lateral aspect: these supply the lower, lateral medulla oblongata. Anastomotic interconnections occur among their smaller branches as they continue on to supply the dorsal aspect of the medulla.

All medially directed branches of the vertebral arteries anastomose freely with one another on the ventrolateral surface of the medulla oblongata.

The Basilar Artery

The median arteria basilaris forms by confluence of the two arteriae vertebrales at the posterior border of the pons. It sends off five pairs of rami ad pontem as it courses cephalad across the pons. The most anterior pair arises immediately caudal to the bifurcation of the basilar artery.

The second pair of branches emanating from the arteria basilaris constitutes the larger arteriae cerebelli inferiores anteriores. The collateral branches supply not only the ventrolateral pons but much of the flocculus as well. As each inferior anterior cerebellar artery crosses the pons, it sends small branches to the base of the trigeminal nerve trunk. The abducens nerve arises just cephalic to the level of the inferior anterior cerebellar artery on each side.

In a well-injected individual (tree shrew 4), one branch of each inferior anterior cerebellar artery can be observed to supply the inner ear region as the arteria labyrinthi. Along the ventral margin of the flocculus, a slender branch anastomoses with a similar branch coursing posteriorly from the superior cerebellar artery. This long anastomotic channel sends off small twigs to both pons and flocculus. Some small branches continue laterally from the posterior choroid plexus area to supply the caudolateral cerebellar hemisphere and deep caudal aspect of the vermis.

All branches of the basilar artery display anastomotic interconnections on the ventrolateral surface of the pons.

The Basilar Artery (Bifurcation)

The bifurcation of the arteria basilaris occurs at the rostral border of the pons. (See Figure 3.) In three of the four tree shrews observed, the bifurcation is quite symmetrical in arrangement of branches. In these cases there is a short truncus communis (one-half to two-thirds of a millimeter in length) on each side. From this trunk the superior cerebellar and mesencephalic arteries diverge laterally, while the main trunk continues to curve rostrally as the posterior communicating artery on each side. In tree shrew 3, such a common trunk is observable on the right side, but not on the left. On the left side, the superior cerebellar artery seems to be the terminal branch of the basilar artery, arising at a right angle to the parent vessel. Then, the somewhat reduced bifurcation product appears to be the proximal portion of the mesencephalic artery, as the latter curves anterolaterally, just rostral to the oculomotor nerve origin. The posterior communicating artery continues the cephalic curve, so that the posterior cerebral artery emerges at a right angle.

The bifurcated arteria basilaris (proximal arteria mesencephali on left side of tree shrew 3) sends off several, slender, parallel rami centrales

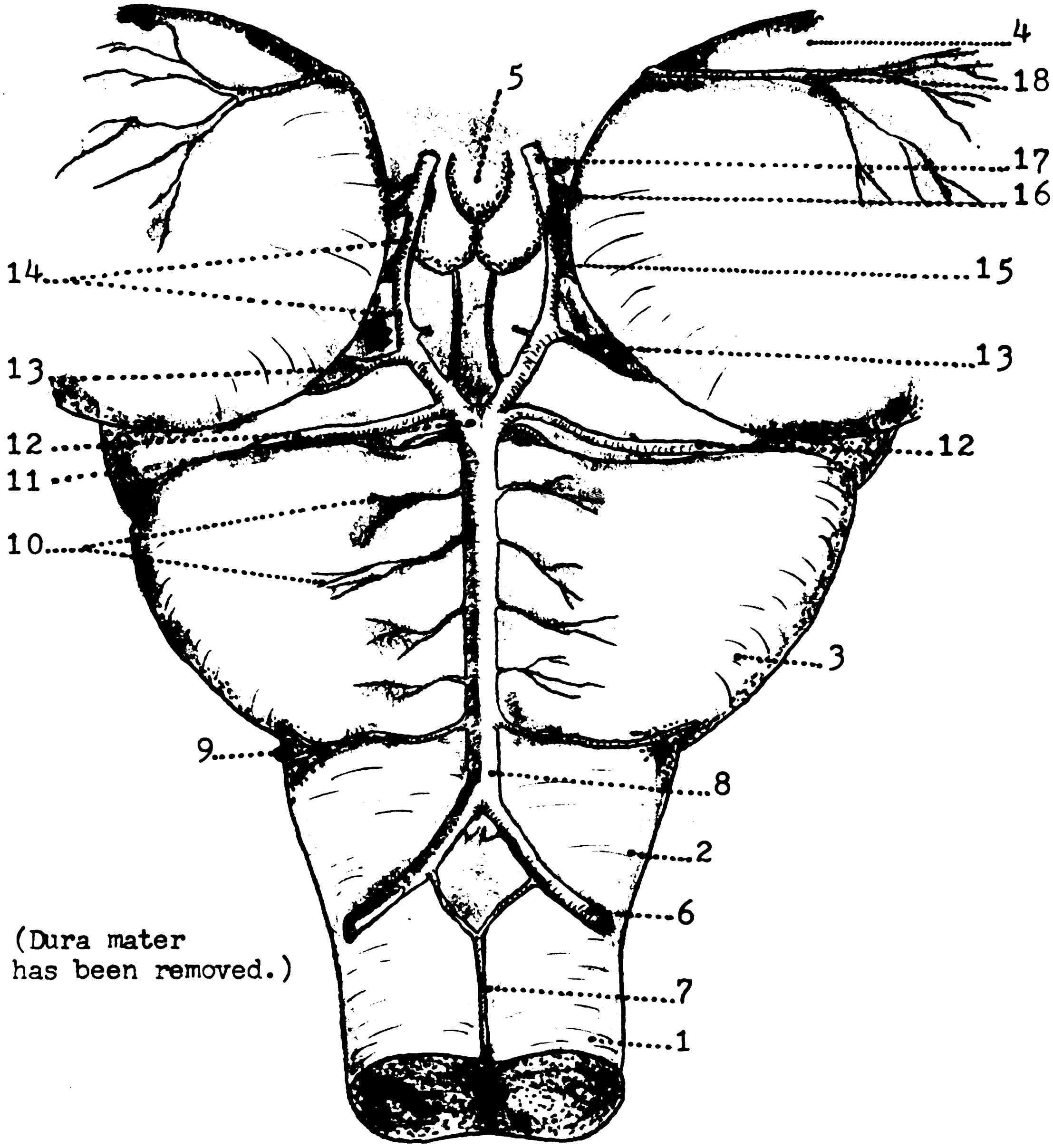


Figure 3. Ventral View of the Brain (Tree Shrew 3).

Key to numbers used: 1, spinal cord; 2, medulla oblongata; 3, pons; 4, cerebrum; 5, hypophysis cerebri; 6, vertebral artery; 7, ventral (anterior) spinal artery; 8, basilar artery; 9, anterior inferior cerebellar artery; 10, pontine arteries; 11, common trunk for right superior cerebellar and mesencephalic arteries; 12, superior cerebellar artery; 13, mesencephalic artery; 14, posterior communicating artery; 15, posterior cerebral artery; 16, cerebral carotid (promontory) artery (cut off); 17, anterior ramus of cerebral carotid artery; 18, a branch of the middle cerebral artery.

entering the posterior perforated substance.

Where a common trunk results from basilar bifurcation, it sends off a large arteria cerebelli superior that is not quite as large as the main continuation of the trunk.

The Superior Cerebellar Artery

The superior cerebellar artery courses laterally along the upper border of the pons to the cephalic aspect of the flocculus, sending collateral branches to the pons, the posterior colliculus, and deep parts of the flocculus. There are three major terminal branches of the superior cerebellar artery. The first of these diverges caudally along the dorsal surface of the flocculus near the junction between the latter and the cerebellar hemisphere, supplying twigs to both and communicating with small branches of the two inferior cerebellar arteries. This branch continues over to the posterior deep aspect of the cerebellar hemisphere, crossing the latter to terminate in branches supplying the posterior deep region of the vermis. This long trunk also sends off collateral branches to the choroid plexus of the fourth ventricle.

The other major terminal branches of the superior cerebellar artery supply the rostral deep surfaces of the cerebellar hemisphere and the vermis. One branch follows a course deep to the transverse venous sinus. The other major branch passes posteriorly between the cerebellar hemisphere and vermis, on the deep surface.

The Mesencephalic Artery

The main continuation of the bifurcated basilar artery appears to be the proximal arteria mesencephali (or the distal arteria communicans posterior) connecting with either the superior cerebellar artery or their shared common trunk. This vessel continues the circulus arteriosus cerebri for another one and one-half to one and three-fourths millimeters, on each side, before the distal mesencephalic artery extends laterad across the ventrolateral midbrain cephalic to the attachment of nervus oculomotorius. This proximal mesencephalic artery (distal posterior communicating artery) sends small twigs to the midbrain and hypothalamus.

The mesencephalic arterial trunk extends laterad one to two millimeters before sending off two to four major branches deep to the overhanging temporal lobe. These branches tend to course in parallel ("penicillus") formation as they ramify further. These continue across the lateral, and then the dorsal, aspect of the midbrain at the level of the anterior colliculus, which is the major area supplied. The most rostral branch of the mesencephalic artery generally follows the groove along the cephalic margin of the anterior colliculus to terminate in the dorsal thalamus region. As this rostral division approaches the dorsal midline, it diverges dorsally to supply the splenium of the corpus callosum. It anastomoses with the more caudal divisions of the mesencephalic artery. It also apparently sends some terminal twigs (arteria choroidea posterior medialis) to the choroid plexus of the third ventricle.

The lower or more caudal divisions of the arteria mesencephali course more directly laterad, obliquely crossing, but not following, the groove between the anterior and posterior colliculi. The main continuation extends obliquely across the anterior colliculus, giving numerous branches to it. A few branches extend as far caudad as the posterior colliculus. This major caudal division forms several anastomoses with branches of the posterior cerebral artery.

The Posterior Communicating Artery

The apparent continuation of the bifurcated basilar artery cephalic to the level of the mesencephalic branch may appropriately be called the arteria communicans posterior. It continues rostrally, lateral to the hypothalamus and deep to the overhanging medial border of the temporal lobe.

The Posterior Communicating Artery--Posterior Cerebral Branch

The arteria cerebri posterior arises one-half to three-fourths of a millimeter cephalic to the arteria mesencephali. Proximally, the posterior cerebral artery sends twigs to the cerebral peduncle. As the posterior cerebral artery courses laterad, it lies parallel with the mesencephalic artery for about two millimeters. Having crossed the cerebral peduncle, the artery diverges cephalolaterally to cross the anterior colliculus and optic tract. Before reaching the optic tract level, the posterior cerebral artery sends off three (two often arising from a common stem) branches that course along the deep surface of the posterior cerebral hemisphere, curve around the caudal margin, and then ramify over the posterior occipital and temporal regions. *En route*, these branches anastomose with mesencephalic branches (on the deep aspect of the hemisphere).

The Posterior Communicating Artery--Anterior Choroidal Branch

In tree shrew 4, what appears to be the arteria choroidea anterior arises from the arteria communicans posterior, about one-fourth of a millimeter rostral to the origin of the arteria cerebri posterior. It courses laterally, deep to the overhanging temporal lobe, and gives off numerous long branches to the posteromedial hemisphere region and posterodorsal thalamus. Many of these branches apparently supply the choroid plexus of the lateral ventricle. (In tree shrews 1, 2, and 3, a comparable vessel arises more rostrally, above the level of the arteria ophthalmica.)

The Circle of Willis--Cerebral Carotid Entrance

The arteria communicans posterior continues its rostral course for two to three millimeters before receiving the arteria carotis interna, of which it is the proximal posterior ramus. *En route*, it sends more branches to the hypothalamic region and to the cerebral peduncle and optic tract. The arteria carotis interna enters the circulus arteriosus cerebri just caudal to the optic tract, as the latter is prolonged caudolaterad from the optic chiasma.

It should be noted, too, that the portion of the arteria communicans posterior between the level of entry of the arteria carotis interna and the exit of the posterior cerebral and mesencephalic arteries is somewhat attenuated in comparison with the bifurcated basilar portion of the circulus arteriosus cerebri more caudally and in comparison with the ramus anterior of the arteria carotis interna more cephalically. These more caudal and cephalic portions are about equal in calibre. If a difference can be detected, the caudal portion appears to be slightly larger.

The Cerebral Carotid Artery--Anterior Ramus

The anterior ramus of the internal carotid artery continues cephalad along the groove between the optic chiasma and the temporal lobe. It continues to send off fine branches to these adjacent structures.

The Ophthalmic Artery

The first longer branch arising from the medial aspect of the internal carotid artery (about one and one-half millimeters rostral to the internal carotid entrance) is the extremely reduced arteria ophthalmica. The latter arises ventral to the optic chiasma, continuing obliquely across the ventral surface of the chiasma and optic nerve to the point of anastomosis with the ciliary trunk of the stapedial artery (superior ramus) on the rostroventral aspect of the nerve near the bulbus oculi. (See Figure 2.)

The Anterior Choroid Artery

In tree shrews 1, 2, and 3, the most prominent branch of the internal carotid artery (anterior ramus), extending laterally across the optic tract, may be regarded as an anterior choroid artery; a sizeable collateral branch continues over to the choroid plexus of the lateral ventricle. The main continuation of this artery ends in the region of the geniculate bodies and the pulvinar of the thalamus.

After coursing rostrally another one-half millimeter, the anterior ramus of the internal or cerebral carotid artery sends off (laterally) a fairly small, but constant, branch supplying the temporal pole area (pyriform lobe) of the cerebral hemisphere.

The Middle Cerebral Artery

Immediately cephalic to this (within one millimeter), the anterior ramus of the internal carotid artery sends off the arteria cerebri media. The latter is almost as large as the main continuation, which is designated as the arteria cerebri anterior.

Coursing craniolaterally, the middle cerebral artery enters the Sylvian fossa of the cerebral hemisphere. Collateral branches supply the entire

fossa area. The main stem continues around the lateral margin onto the superolateral surface of the hemisphere, where the main stem continues mediocaudally. Its collateral branches supply the upper temporal and much of the parietal areas, to within three millimeters of the longitudinal fissure. The remaining medial strip is supplied by branches of the anterior cerebral artery. The branches supplying the superolateral portions of the frontal lobe originate from the part of the middle cerebral artery lying within the Sylvian fossa; thus these branches must curve around the lateral border of the hemisphere individually. They supply all but the most medial two millimeters of the dorsal area of the frontal lobe. The remaining medial strip is, again, supplied by branches of the anterior cerebral artery.

Some rostrally directed branches of the middle cerebral artery (within the Sylvian fossa region) supply the proximal portions of the olfactory tract.

The middle cerebral artery sends off a pair of branches (more or less at right angles) to course rostrally and caudally in the rhinal sulcus. This sulcus continues well back into the temporal lobe region.

The Anterior Cerebral Artery

The anterior cerebral arteries and the anterior communicating artery send out small twigs of supply to the optic chiasma.

Immediately cephalic to the optic chiasma, the arteria communicans anterior transversely interconnects the two arteriae cerebri anteriores. The right half may be somewhat larger in caliber than the left, or the reverse. The arteria communicans anterior gives off, at right angles to itself, the single, median arteria cerebri anterior communis (arteria corporis callosi) that courses dorsally over the anterior surface of the rostrum of the corpus callosum. On reaching the dorsal surface of the corpus callosum, this common anterior cerebral artery bends posteriorly to course along the upper surface of the corpus callosum. The collateral branches given off en route supply the medial surfaces of the frontal lobe areas. (No branches extend rostrally to supply the olfactory bulbs.)

About one-third of the distance back along the upper surface of the corpus callosum, the common anterior cerebral artery begins a dorsocaudal ascent, away from the corpus callosum and toward the dorsal surface of the cerebrum, within the longitudinal

fissure. En route, it gives off additional branches to the medial surfaces of the hemispheres. The major branches curve around the dorsomedial margin of the cerebral hemisphere to supply the medial two to three millimeters of the dorsolateral surfaces.

As the common anterior cerebral artery nears the dorsal surface (while still within the longitudinal fissure), it bifurcates into two equal-sized branches (often referred to as arteriae corporis callosi) about half-way back along the length of the corpus callosum. Each branch ascends over the dorsomedial border of the hemisphere to supply the medial three millimeters of the dorsum of each hemisphere. (This distribution is apparent in latex-injected specimens. Anastomoses among the branches of the anterior, middle, and posterior cerebral arteries occur on the dorsolateral surfaces of the cerebral hemispheres. In tree shrew 4, with the more pervasive Microfil injection, the three areas of distribution are not readily distinguishable because of the high degree of overlap in areas of branching.)

The apparent continuation of the anterior cerebral arteries, rostral to the level of the anterior communicating artery, sends branches of supply only to the olfactory tract and bulb; thus they may be called arteriae bulbi olfactorii mediales.

Shortly after exit of the arteria cerebri media, each arteria cerebri anterior gives off a ramus ethmoidalis or arteria bulbi olfactorius lateralis that courses rostrad to reach the lamina cribrosa, where it connects with an intradural rete ethmoidale. The ramus orbitalis from the arteria infraorbitalis and the ramus ethmoidalis from the arteria stapedia, joining within the orbit, form a common ethmoidal branch that also connects with this rete ethmoidale. From the rete, in turn, small branches extend into the nasal cavity with the fila olfactoria; thus blood from the arteria carotis cerebri may reach the nasal mucosa, with its exceedingly rich plexus of vessels.

The arteria bulbi olfactorius lateralis also sends branches to the lateral aspects of the olfactory tract and lobe. Its terminal branches anastomose with those of the arteria bulbi olfactorius medialis and with cephalic branches of the arteria cerebralis media.

DISCUSSION

There is no characteristic arrangement of cranial arteries for a given order of mammals: certain types are repeated in several orders; animals in closely related groups frequently present very different conditions. Thus, one cannot trace alterations through a serial progression of phylogenetic stages (Tandler, 1899; Hofmann, 1900; de Vriese, 1905; Stephan, 1954; Guthrie, 1963).

There is, nevertheless, in the class Mammalia, a basic cranial arterial pattern, in terms of which variant types may be interpreted. Retention of one portion or obliteration of another portion of the vascular system in different animal groups cannot yet be explained. Studies of what may be called the "ecology" of head structures are required. When all the facets of the dynamic processes of development of this head complex are clarified, laws of head structure will emerge. Thus, effort expended in gathering and correlating comparative data will be repaid.

Discussion of the tupaiid arteries, from a phylogenetic point of view, here follows in the same sequence as in the preceding section on descriptive anatomy.

The Arch of the Aorta

The pattern of branching of the aortic arch in *Tupaia glis*--with two brachiocephalic trunks or with left common carotid and left subclavian trunks arising separately from the aorta--is a rather generalized, and possibly close-to-primitive, condition among mammals.

Observations of other anatomists on Tupaiidae are noted here. In the two specimens of *Ptilocercus lowii* examined by Le Gros Clark (1926a), there was a (right) brachiocephalic artery (about six millimeters in length) and a very short (one-half millimeter to two and one-half millimeters in length) left brachiocephalic trunk for the left common carotid and left subcalvian arteries. Le Gros Clark (1926a) stated that the occurrence of a short brachiocephalic trunk on the left side is usual in *Tupaia*. Recognizing variation, he observed (1926a) one specimen of *Tupaia minor* in which the left common carotid and left subclavian arteries had separate origins from the aortic arch.

Platzer (1960) cited Hill and Davies as having observed, in *Tupaia glis* (number of specimens not given), a pattern that represents a further step

in the concentration of branches in the (right) brachiocephalic trunk. Here, on one side, there is a common trunk for the (right) brachiocephalic and the left common carotid arteries. On the other side is found the left subclavian artery. This would resemble the most common human variant.

Among Marsupialia, examples of the greatest separation of trunks are found correlated with symmetry of spacing. *Phascolarctos* (marsupial bear) may have four separate trunks; *Thylacinus* (Tasmanian wolf) may show two subclavian trunks and an intervening bicarotid trunk (Parsons, 1902).

Considerable symmetry is also displayed among Insectivora and Chiroptera, the most primitive eutherian orders (Parsons, 1902). A left brachiocephalic artery (of varying length) has been commonly observed among bats (*Vesperugo*, *Plecotus*, *Pteropus*, *Cynonycteris*) (Grosser, 1901; Parsons, 1902). In other bats (*Rhinolophus*, *Vespertilio*), the left common carotid stem arises separately, but closer to the left subclavian than to the (right) brachiocephalic artery (Grosser, 1901; Årnbäck-Christie-Linde, 1907). A symmetrical arrangement with two brachiocephalic trunks is also the more common arrangement among Insectivora, being usual in *Talpa* (mole) and very frequent in *Chrysochloris*

(golden mole) and Erinaceus (hedgehog). The common variant in the latter two genera is that in which the left common carotid lies closer to the left subclavian than to the (right) brachiocephalic trunk (Dobson, 1882-1890; Parsons, 1902). This latter situation is regularly found in other insectivores, such as Centetes, Myogale, Potamogale, Rhynchocyon, and Soricidae (Dobson, 1882-1890; Parsons, 1902; Årnbäck-Christie-Linde, 1907). Other primitive mammals in which the latter arrangement is common or the rule would include armadillo, three-toed sloth, and aard-vark (Parsons, 1902). As a variant in some of these forms, the left common carotid artery may lie closer to the brachiocephalic than to the left subclavian artery. Monotremata commonly are included in the latter group (Parsons, 1902; Årnbäck-Christie-Linde, 1907).

The possible sequence of patterns is suggested by Lewis's (1923) study of sheep embryos. He found that aortic branches pass from an early symmetrical condition, through asymmetrical phases, to reach the adult pattern of maximum concentration of branches typical for ungulates.

Based on generality of presence in most mammalian orders (as rule or as variant) one might, however, tend to regard the asymmetrical, three-trunk pattern as more primitive than two-trunk or four-trunk patterns (de Garis, 1941).

Among higher Primates, the situation closest to the above-described "primitive" patterns would be that with three trunks, the left common carotid artery lying near the brachiocephalic trunk. This is the predominant arrangement in Homo, Gorilla, Pan, Cebus (capuchin), Callithrix (marmoset), Ateles (spider monkey), and Saimiri (squirrel monkey) (Owen, 1866; Sonntag, 1923, 1924; Beattie, 1927; Glidden and de Garis, 1936; Hill and Davies, 1959; Platzer, 1960).

Most prosimians appear to be more specialized. The only prosimians regularly displaying the three-trunk arrangement are Tarsius (Woollard, 1925; Hill, 1953a; Platzer, 1960) and Loris (Chapman, 1900; Rau and Rao, 1930; Davies, 1947; Hill and Davies, 1959). This is a common variant in large mammalian orders, such as Carnivora and Rodentia (Parsons, 1902).

The general arrangement in Lemuriformes is the two-trunk pattern, in which the (right) brachiocephalic and left subclavian trunks arise from the aortic arch (Chapman, 1900; Davies, 1947; Hill, 1953b; Hill and Davies, 1959; Platzer, 1960). This two-trunk arrangement is also the usual one for a number of higher Primates, such as Hylobates (gibbon), Macaca, Alouatta (howler monkey), Mandrillus, Pongo (orang-utan) (Chapman, 1900; Sonntag, 1922; Lineback, 1933; Platzer, 1960).

Primates illustrate well, within the range of their variation, the seemingly general mammalian trend toward concentration of trunks on the right by fusion with the (right) brachiocephalic trunk. This reaches its peak in the pattern (uncommon anomaly in Lemur, usual situation in Propithecus) showing a single (right) brachiocephalic trunk arising from the aorta (Hill and Davies, 1959).

Although concentration of branches is highly correlated with narrow thoracic outlet and increasing distance of the aortic arch from that outlet (Parsons, 1902; Sawin and Edmonds, 1949), it does not seem indifferent that the shift has been to the right--as for veins--in the heart region. There may be correlation between heart orientation within the thorax and the asymmetrical concentration of trunks on the right. Man is closer to the primitive primate condition (neotenic?) than many lemurs known to be specialized (as primates) in other ways.

With respect to branching of the adult aortic arch, Tupaia glis is like many Insectivora, but most closely resembling those showing the trend (primate and general mammalian) toward asymmetry with concentration of branches on the right.

The Common Carotid Artery (Bifurcation)

The level of bifurcation of the common carotid artery is of no special phylogenetic significance. In most primitive mammals, the division into external and internal carotid arteries occurs deep to the musculus digastricus or just caudal to this. This applies to Tupaiidae, Prosimii, Insectivora (except *Talpa*, with division occurring deep down in the neck), Chiroptera, Rodentia, and Marsupialia. In Monotremata and Edentata, the bifurcation tends to be somewhat lower, lying opposite the hyoid bone or the larynx (Tandler, 1899, 1901; Grosser, 1901; Sicher, 1912; Hafferl, 1919; Woollard, 1925; Le Gros Clark, 1926a; Davies, 1947; Hill, 1953a, 1953b; Platzer, 1960).

The External and Internal Carotid Stems (Relative Size)

The relative sizes of the external and internal carotid arterial stems may be of some phylogenetic significance when more facts are known.

In Tupaiidae the external and internal carotid arteries are approximately equal at their origin. According to Hill (1953b), the external carotid is by far the larger of the two arteries in Strepsirhini.

Davies (1947) confirmed this for *Nycticebus*. Tandler (1899) found the two vessels to be about equal in size for *Loris* (*Stenops*) *gracilis* and *Galago* (*Otolicnus*) *senegalensis*. In *Daubentonia* (*Chiromys*) *madagascariensis* and *Lemur varius* there is a rudimentary internal carotid artery and a normal external carotid artery (Tandler, 1899; Hill, 1953b). In *Tarsius*, however, the external carotid, as such, is much smaller than the internal carotid artery (Platzer, 1960). This is misleading since a number of typically external carotid branches arise from a separate common trunk at the bifurcation point (Hafferl, 1919; Woollard, 1925; Hill, 1953a).

There is also variability in this feature among Insectivora. Whereas in *Erinaceus europaeus* the two arteries are almost equal in size, in *Talpa europaea* the internal carotid is markedly larger than the external carotid artery (Tandler, 1899).

In *Pteropus* (Chiroptera), the two vessels are approximately equal in size (Grosser, 1901), as also in *Ornithorhynchus* (Monotremata) and Edentata (Tandler, 1899). The external is larger than the internal carotid artery in *Echidna* (Monotremata) and in Marsupialia (Tandler, 1899; 1901).

The variation in size of external and internal carotid stems depends upon two principal factors: (1) the relative share of internal carotid and vertebral arteries in supplying the circulus arteriosus cerebri and (2) the degree of (adult) development of the stapedial branch of the internal carotid artery. In lizards, possessing the primitively limited distribution of the external carotid artery and the rudimentary intracranial development of vertebral arteries, the internal carotid artery is at least twice the size of the external carotid artery (Bhatia and Dayal, 1933).

The External Carotid Artery (Relations with the Stapedial Branch of the Internal Carotid Artery)

The external carotid artery of lower vertebrates is weak: its distribution area is limited, in amphibians and lizards, to the hyoid and tongue musculature, some muscles of mastication and the pharynx wall, and subcutaneous connective tissue of the lower lip and region medial to the mandible (Bhatia and Dayal, 1933; Stephan, 1954). Thus, in the primitive tetrapod condition, the arteria carotis externa is essentially an arteria lingualis. It has been noted that the lingual artery differentiates very early in the mammalian embryo (Grosser, 1901; Tandler, 1902; Sicher, 1912; Hafferl, 1919). During embryogenesis of higher mammals, anastomoses form in such a manner as to permit take-over by the arteria carotis externa of branches (primarily, arteria stapedia) of the internal carotid system (Tandler, 1899; Stephan, 1954).

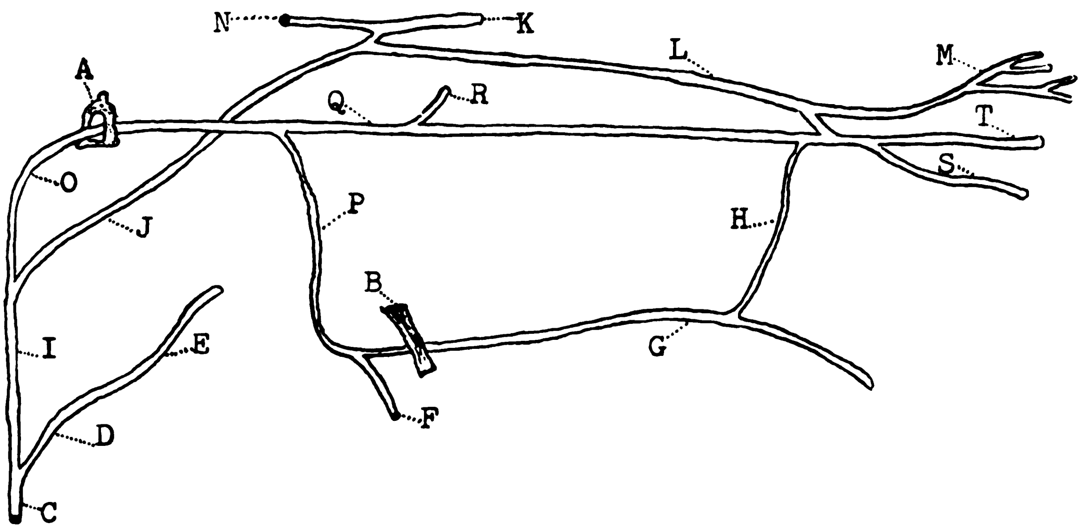
Preliminary to further discussion of the external carotid artery, the phylogenetic role of the stapedial branch of the internal carotid artery must be indicated.

The arteria stapedia is a primary artery of the mammalian embryo (Grosser, 1901; Tandler, 1902; Evans, 1912; Sicher, 1912; Hafferl, 1919; Congdon, 1922). Its precursor is found in lower vertebrates: in the lizard, <u>Hemidactylus flaviviridis</u> (Bhatia and Dayal, 1933), the stapedial artery arises from the internal carotid artery at the posterior end of the ear. Although the stapedial artery sends off a small auricular branch, its two major rami show a distribution similar to that observed in primitive mammals. The more dorsal ramus (temporal artery) supplies occipital and temporal regions (still lacking branches from the external carotid artery) and then presents a pattern very similar to the supraorbital division (superior ramus) in mammals; that is, it enters the orbit to send off lacrimal, ophthalmic, and frontal branches. The second major ramus (mandibular artery) of the lizard's stapedial artery is comparable in distribution with the inferior ramus of primitive mammals and mammalian embryos; thus it has a branch comparable with the inferior alveolar artery and one branch (superficial ophthalmic artery) resembling the mammalian infraorbital artery in its distribution. Of great interest is the presence of an anastomosis interconnecting the mandibular ramus and the external carotid artery. A similar anastomosis occurs very early in mammalian embryos (Grosser, 1901; Tandler, 1902; Evans, 1912; Sicher, 1912; Hafferl, 1919).

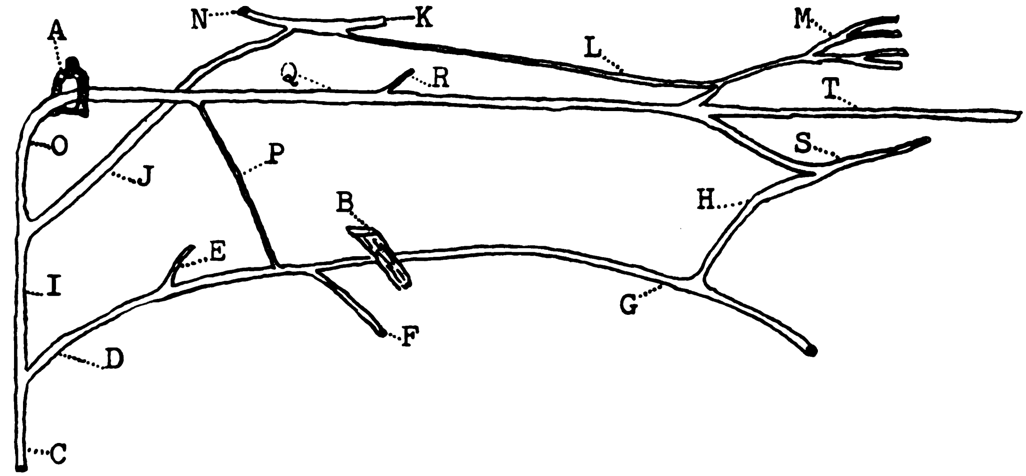
The simplest adult mammalian external carotid pattern is found in Monotremata (Tandler, 1899, 1901). The arteria carotis externa is not yet completely differentiated as to its branches, especially in *Ornithorhynchus*. The latter genus lacks an arteria maxillaris (interna). The arteria stapedia, arising below the tympanic cavity, still sends a branch to occipital-artery territory. Medial to the nervus trigeminus, the inferior ramus of arteria stapedia receives the slender ramus anastomoticus from the arteria carotis externa. On emerging from the pterygoid canal, this inferior ramus bifurcates into the ramus infraorbitalis (accompanying nervus infraorbitalis into the face) and the ramus orbitalis that apparently supplies all structures of the orbit except the bulbus oculi. In the absence of a superior ramus, there are no supraorbital branches. (There is, however, good presumptive evidence of the presence of the superior ramus in Echidna; thus embryonic presence of both rami of the arteria stapedia is assumed for Monotremata.) (Tandler, 1899, 1901)

Marsupialia, including Didelphis, show the direct continuation of the arteria carotis externa in the form of a typical (similar to human) arteria maxillaris (interna). Embryonically, it represents the distal (to mandibular division of nervus trigeminus) portion of the inferior ramus of arteria stapedia. As flow through the arteria carotis externa increased, the proximal inferior ramus of arteria stapedia evidently atrophied. This pattern is typical for most Eutheria, including all Primates (Tandler, 1899, 1901).

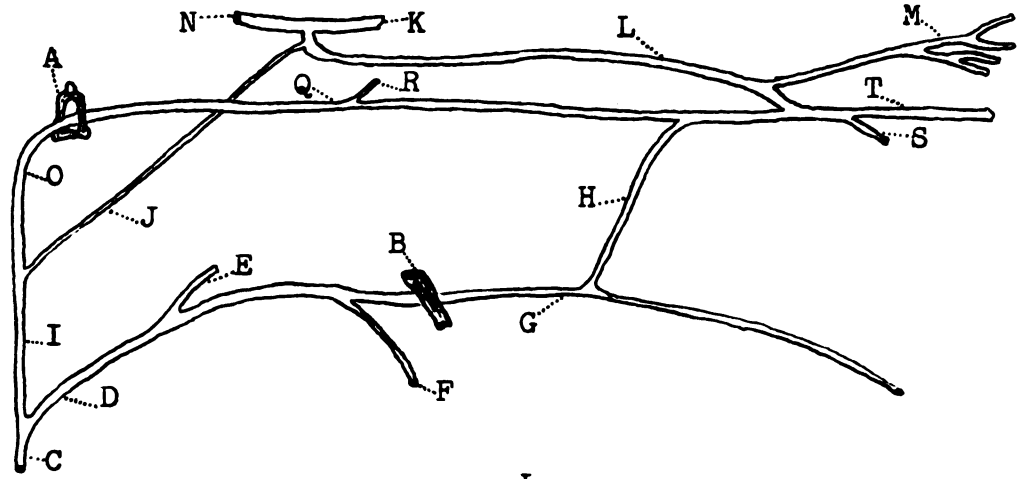
In this respect, some Insectivora appear to be more primitive than Marsupialia; secondary reversion is another possibility. In Erinaceus europaeus (hedgehog) and Talpa europaea (mole), the arteria carotis externa does not continue as an arteria maxillaris. (See Figure 4.) Since the arteria stapedia is initially strong and the arteria carotis externa weak among mammals, atrophy of the proximal inferior ramus (arteria stapedia) would not



Erinaceus



Tupaia



Lemur

Figure 4. Carotid Arterial Branching Patterns.

Figure 4. Key to letters used:

A	stapes
B	mandibular ramus of the trigeminal nerve
C	common carotid artery (stem)
D	external carotid artery (stem)
E	superficial temporal artery
F	inferior alveolar artery
G	infraorbital artery
H	orbital ramus of the infraorbital artery
I	internal carotid artery (stem)
J	cerebral carotid (promontory) artery
K	anterior ramus of the cerebral carotid artery
L	ophthalmic artery
M	ciliary artery (ramification)
N	posterior ramus of the cerebral carotid artery
O	stapedial artery (stem)
P	(proximal) inferior ramus of the stapedial artery
Q	superior ramus of the stapedial artery
R	middle meningeal artery
S	ethmoidal artery
T	frontal artery

be expected. In the hedgehog and mole, even the connection between them evidently breaks down (by obliteration of a part of the arteria carotis externa proximal to the anastomosis with the ramus inferior of arteria stapedia) (Sicher, 1912). Thus, the arteria carotis externa ends as the arteria temporalis superficialis in _Erinaceus europaeus_. The stapedial inferior ramus retains the anterior mandibular and infraorbital territories (including probable embryonic take-over, by anastomosis, of the inferior alveolar artery) (Sicher, 1912). The involution of the arteria carotis externa goes a step further in _Talpa_, in which even the superficial temporal artery has become part of the stapedial system (Tandler, 1899; Sicher, 1912).

In _Suncus murinus_ (Soricidae) (Sharma, 1958) the pattern conforms with that of _Ptilocercus_ (Le Gros Clark, 1926a) and at least some _Tupaia glis_ individuals (present study). That is, the proximal stem of the inferior ramus (arteria stapedia) persists in direct continuity with the arteria maxillaris. (See Figure 4.)

In general, Insectivora most nearly retain the basic embryonic pattern for mammals. Some tupaiids and soricids retain it completely. In hedgehog and mole, the inferior ramus (arteria stapedia) is

retained completely; a portion of the arteria carotis externa has been lost, apparently by secondary regression. The attenuation and possible discontinuity observed in tupaiids may represent an incipient primate trend; it is also a rather general eutherian trend, leading to such forms as edentates, ungulates, some carnivores, and some bats.

It is of interest that a phase of development similar to that described by Sicher (1912) for *Talpa* also occurs in *Tarsius* (Prosimii) (Hafferl, 1919); thus there appears to be, at least in some primate embryos, an early phase of rapid extension of the arteria carotis externa, followed by a growth lapse in which connection with the arteria stapedia is lost and finally by a marked lengthening of the arteria carotis externa to re-establish connection. The last one of these three phases is evidently lacking in *Talpa* and *Erinaceus*. The three-step succession has been observed also in the pig by von Hofmann (1914) and in bats by Grosser (1901). In certain Rodentia (*Mus* and *Pedetes*) the arteria carotis externa has also lost connection, in adult, with the arteria maxillaris (Tandler, 1899).

The status of *Tupaia glis* appears (without benefit of embryological study) to be as primitive as that of any mammal. Like Insectivora, it retains both superior and inferior rami of arteria stapedia as well as the anastomosis of the latter with the arteria carotis externa. This anastomosis, present in Ptilocercus, may be lacking or interrupted in some Tupaia individuals, at least in the (serially sectioned) specimen of Tupaia minor observed by Le Gros Clark (1926a). In contrast with Erinaceus and Talpa, among Insectivora, the arteria carotis externa of Tupaiidae does continue as an arteria maxillaris.

The principal difference between Lemur varius and Tupaia glis is the loss, in Lemur, of the proximal stem of the inferior ramus of arteria stapedia. (See Figure 4.) Otherwise, both show a well-developed stapedial system and continuation of the arteria carotis externa as an arteria maxillaris (Tandler, 1899). In this pattern the arteria meningea media remains definitively attached to the superior ramus of arteria stapedia. This is also the case in Nycticebus (Davies, 1947) and Daubentonia (Chiromys) (Platzer, 1960).

The Maxillary Artery (Pterygoid Portion)

A feature of unknown phylogenetic significance is the path taken by the pterygoid portion of the arteria maxillaris through an external alisphenoid canal in Tupaia glis. The external alisphenoid process and its canal are very small. The arteria maxillaris seems to deviate mediad to enter it and no visible branches are given off by the artery within the canal. An external alisphenoid canal is present in some insectivores (*Gymnura*, *Centetes*, *Myogale*, and Solenodontidae) and absent in others (*Erinaceus*, Potamogalidae) (Dobson, 1882-1890). This canal may or may not be present in Macroscelididae (Muller, 1935; Evans, 1942). It is also present in elephants, some Carnivora, and some Perissodactyla (Turner, 1848). Thus, an external alisphenoid canal is probably a primitive mammalian feature. Since it has no apparent function in Tupaiidae, it seems most reasonable to regard it as a vestige. When present in living mammals, it evidently transmits a (masticatory) muscle branch of nervus trigeminus (Turner, 1848). It is of interest that in some bats and rodents the (internal) maxillary artery runs through the cranial cavity for a part of its course (Grosser, 1901; Guthrie, 1963). The ramus inferior of arteria stapedia may formerly have had a more medial position.

The Infraorbital Artery--Ramus Orbitalis

On reaching the orbit, the arteria maxillaris of *Tupaia glis* becomes the infraorbital artery. This is the characteristic pattern for many mammals, including Marsupialia, Insectivora, and Primates.

The orbital ramus, generally present, is a collateral branch of the infraorbital artery. In Marsupialia and in higher Primates the ramus orbitalis takes the form of a few small muscle branches (Tandler, 1899).

In *Tupaia glis* the ramus orbitalis of arteria infraorbitalis joins the ethmoidal branch of the superior ramus of arteria stapedia just outside of the foramen conducting the arteria ethmoidalis into the anterior cranial cavity (region of the olfactory lobe). (See Figure 4.)

The only comparable description found in the literature is that for *Tarsius*. Hill (1953a) described a large branch of the infraorbital artery that courses across the floor to the medial wall of the orbit, where it ramifies over the os planum and sends one of these branches through the ethmoidal foramen.

Tandler (1899) simply described the large ramus orbitalis of *Lemur varius* as arising in the infratemporal fossa and joining the superior ramus of arteria stapedia. (See Figure 4.) In *Daubentonia* (*Chiromys*) *madagascariensis* a ramus orbitalis is not demonstrable. In *Loris* (*Stenops*) *gracilis* and *Galago* (*Otolicnus*) *crassicaudatus* the ramus orbitalis is reduced to a small muscle branch.

In rodents and bats the orbital ramus is more variable in its point of origin from the arteria carotis externa or its terminal continuation as the arteria maxillaris and the arteria infraorbitalis. In many bats it is the major vessel of the orbit, often referred to as the arteria ciliaris communis, equalling arteria infraorbitalis in size (Grosser, 1901; Guthrie, 1963).

The Internal Carotid Artery (Stem and Major Ramification)

The arteria carotis interna is a primary artery in all vertebrates. As expected, it is well-developed in Monotremata and Marsupialia, most Insectivora (known exceptions: *Suncus murinus* and probably some *Tupaia* species), most Primates (known exceptions: *Lemur* and *Daubentonia* species), as well as some members of many other orders (Edentata, Perissodactyla, Pinnipedia, Carnivora, Rodentia, Chiroptera) (Tandler, 1899, 1901; Le Gros Clark, 1926a; Stephan, 1954; Sharma, 1958).

Even when the internal carotid supply to the brain is reduced or virtually absent, the initial portion giving rise to the stapedial artery remains well developed; examples include lemur, aye-aye, horseshoe bat, and guinea pig (Tandler, 1899; Grosser, 1901). Reduction usually occurs at a relatively late stage of embryonic life (Wolff, 1938).

The primitive mammalian internal carotid artery had four principal branches: (1) the medial entocarotid artery, (2) the promontory artery, (3) the superior ramus of the stapedial artery, (4) the inferior ramus of the stapedial artery (van Valen, 1965).

The Internal Carotid Artery-- Medial Entocarotid Branch

The medial entocarotid artery (typically entering the cranium at the junction between petrosal and basioccipital-basisphenoid bones) is most commonly lost. It is not present in Recent Tupaiidae (van Valen, 1965; McKenna, 1966). Although usually said to be absent in all Recent Primates, Saban (1963) has observed a *carotide antérieure* in *Cheirogaleus* (dwarf lemur). This vessel has the appropriate location and pathway for a medial entocarotid artery. Further, the *rameau tubaire* of *Lemur* is possibly a persistent adult branch of a medial entocarotid artery. There is also some speculation that the medial branch of the internal carotid artery is not the promontory artery (as in other Primates) but, rather, is the medial entocarotid artery (van Valen, 1965).

Although it has been postulated that rodents have descended from an early primate stock (McKenna, 1961), Plesiadapis (earliest known primate skull of the late Paleocene epoch) did not possess a medial entocarotid artery (McKenna, 1966). The artery occurs in some Recent rodents (Guthrie, 1963).

Oligocene leptictids (at a time when primates had already diverged from this stock) possessed a reduced medial entocarotid artery as well as an unreduced lateral branch giving rise to promontory and stapedial arteries (van Valen, 1965; McKenna, 1966).

Based on the observations cited and Tandler's (1899) finding that loss of a medial entocarotid artery is common among Eutheria, it is quite possible that the loss of this artery has occurred independently in the history of Primates and Tupaiidae.

The Internal Carotid Artery--Promontory (Cerebral Carotid) Branch

Of some phylogenetic interest is the size of the promontory artery (the branch of the internal carotid artery that generally joins the circulus arteriosus cerebri in modern tupaiids and primates).

In Leptictidae (of the Oligocene epoch) the lateral branch of the internal carotid artery divided at the promontorium into two large vessels: stapedial and promontory arteries. This pattern persisted in the Microsyopidae (resembling *Plesiadapis*) and in primitive Primates, such as *Plesiadapis*, *Necrolemur*, and *Tarsius* (McKenna, 1966). The large calibre of the promontory artery has persisted in all Recent Primates except *Lemur* and *Daubentonia*, as well as other Madagascan lemurs, including *Hapalemur*, *Lepidolemur*, *Microrhynchus*, *Propithecus*, and *Lichanotus* (Hill, 1953b; Winge, 1941).

Sharma (1958) has observed that *Suncus murinus* (Soricidae), the house shrew of India, is at least one modern insectivore possessing a promontory artery of small diameter correlated with a stapedial artery of greater diameter.

There is some apparent variation among Tupaiidae. In *Ptilocercus* the promontory and stapedial arteries are about equal in size. This also is the case for *Tupaia glis* specimens observed in the present study. However, the promontory artery has been generally described as reduced in calibre (not more than one-third of the diameter of the stapedial artery) and thus comparable with that of lemurs (Le Gros Clark, 1926a; Saban, 1956-1957). Saban (1963) has demonstrated that the stapedial artery of lemurs may be quite reduced or even absent. In any case, lack of special resemblance of tupaiids to lemurs does not preclude tupaiid-primate affinity.

The Internal Carotid System (Relation to Tympanic Walls)

Another phylogenetic issue is the freedom with which the internal carotid system conducts itself through the ear region in relation to the bony walls.

The primitive condition, present in the ultimate primate ancestors, was that in which the internal carotid artery and its branches coursed through grooves; hence "free." In *Plesiadapis* (late Paleocene) the artery ran through an open groove (McKenna, 1966).

In Oligocene leptictids there was still a groove for the internal carotid artery. The trench, to be sure, became quite deep as the promontory artery approached the foramen into the cranial cavity but has been observed to close over (only briefly), in one known fossil specimen, near the bifurcation into promontory and stapedial branches (McKenna, 1966).

Early Tertiary insectivores generally displayed similar grooves (McKenna, 1966).

Thus, although both modern Primates and Tupaiidae have the internal carotid system completely enclosed within bony tubes in the medial wall of the tympanic cavity, the condition probably arose independently in these two groups. Actually, such bony enclosure (partial or complete) must have been a common evolutionary trend occurring in other groups: some Pantolestidae (short-lived side branch of Proteutheria) and some members of modern Erinaceidae, Chrysochloridae, Talpidae, and Macroscelididae (van Kampen, 1905; McKenna, 1966).

The location of the carotid foramen, opening into the bulla, although common to tupaiids and lemurs, is a common one among mammals generally (van Valen, 1965).

The Internal Carotid Artery--Stapedial Branch

Basically, the stapedial branch of the internal carotid artery has long been the artery accompanying the trigeminal nerve ramification (Tandler, 1899).

In the lizard, *Hemidactylus flaviviridis*, where the internal carotid artery lies on the dorsal side of the basisphenoid bone it sends one branch into the cranial cavity while the major portion diverges somewhat to continue anteriorly, sending branches to the masseter muscle, palate, nose, and maxilla (Bhatia and Dayal, 1933).

In another lizard, *Crotaphytus collaris*, Burda (1966) described the internal carotid artery as passing through a canal in the floor of the basisphenoid bone. Just before entering the cranial cavity, it sends off a large naso-palatine branch running laterad through a foramen in the antero-lateral wall of the canal and then sends branches to the floor of the orbit, the nasal region, and the palate.

Tandler's (1902) embryological study of the rat indicated that although the stapedial artery originates from the second aortic arch, it takes over the branches of the primitive mandibular (first arch) artery, giving rise to the supraorbital, infraorbital, and mandibular arteries. (The external carotid artery annexed the mandibular artery later.)

In the primitive state, therefore, the branches of the first branchial-arch artery accompany the divisions of the trigeminal nerve. These peripheral branches would not alter if only the main stem of the primitive mandibular artery was to be replaced by the stapedial artery. In that case the supra-orbital division of arteria stapedia would have an extensive intracranial course from petrous bone to orbit. This is observable in such primitive forms as <u>Lemur</u>, <u>Erinaceus</u>, <u>Talpa</u>, and <u>Arctomys</u> (Tandler, 1899), as well as in Tupaiidae. This may also have been true in some degree for the infraorbital ramus (lizards and some rodents), and to a slight degree for the mandibular ramus (branches to muscles of mastication emerging through the cranial wall in a number of primitive mammals) (Tandler, 1899; Guthrie, 1963). The presumably vestigial alisphenoid canal of *Tupaia* may be most plausibly explained on this assumption since it still probably conducts a small nerve to a masticatory muscle (Turner, 1848).

The Internal Carotid Artery--Inferior Ramus of the Stapedial Branch

Loss of the proximal inferior ramus of the stapedial artery may have occurred independently along primate and tupaiid lines. In the ontogeny of all Primates the proximal stem of this vessel atrophies and the distal ramification is taken over by the external carotid artery (Tandler, 1902; Hafferl, 1919). This may also be the case in some *Tupaia* species or individuals, as indicated by the present study and by Le Gros Clark's observations (1926a). However, in *Ptilocercus* and most *Tupaia glis* specimens observed here the proximal stem of the stapedial inferior ramus persists in the adult, if only as a very slender anastomotic connection with the maxillary artery. It also persists in *Suncus murinus* (Soricidae), according to Sharma (1958). No evidence is available for *Dendrogale* (smooth-tailed tree shrew), which Davis

(1938) regarded as more primitive than Tupaia and slightly less primitive than Ptilocercus in general structural features.

The Internal Carotid Artery-Superior Ramus of the Stapedial Branch

In mammals the primitive distribution areas of arteria stapedia included the upper jaw, the orbit, and the dura mater, as well as peripheral regions of the lower jaw. The ramus superior of arteria stapedia is essential to development of the arteria meningea media and the orbital arteries. Although the distal ramification of these vessels may become secondarily attached to some other definitive parent vessel, the ramus superior of arteria stapedia served as their original stem (Tandler, 1899). Only on this assumption can many peculiar secondary conditions and anomalies be explained. The limited evidence from embryology of representative forms reaffirms this view (Tandler, 1902, 1906; Grosser, 1901; Hafferl, 1919; Wolff, 1938; de la Torre and Netsky, 1960).

The Middle Meningeal Artery

Upon entering the cranial cavity (posterior corner of middle cranial fossa) the ramus superior of arteria stapedia sends off the arteria meningea media in Tupaia glis, as in a number of other

primitive mammals: *Talpa*, *Erinaceus*, *Suncus* (Insectivora); *Daubentonia*, *Lemur* (Primates); *Vespertilio*, *Noctilio*, *Plecotus*, *Phyllostoma*, *Mormoops*, *Taphozous* (Chiroptera); *Rattus*, *Sciurus*, *Marmota* (Rodentia). (See Figure 4.) The main stem of the intracranial portion of the superior ramus of arteria stapedia then continues its subdural course anteriorly to reach its terminal orbital ramification (Tandler, 1899, 1901; Grosser, 1901; Sharma, 1958). This pattern conforms most closely with the primary embryological condition of the ramus superior of arteria stapedia (Grosser, 1901; Tandler, 1902).

Monotremata, Marsupialia, and Edentata are not included in this primitive group. These animals show an apparent loss of the ramus superior (arteria stapedia) as adults. In lower mammals generally there is a tendency for the occipital artery to remain as a branch of the arteria carotis interna, arising just below the posterior skull base. The arteria (stylo)mastoidea, a branch of the arteria occipitalis, takes over the distal ramification of the superior ramus of arteria stapedia in its middle meningeal and orbital portions. This distal portion of arteria occipitalis is often called the arteria diploëtica magna in these three primitive, but aberrant, groups (Tandler, 1899, 1901).

A more usual modification among mammals, and likewise probably acquired in parallel more than once, is an apparent secondary attachment of the arteria meningea media to the arteria maxillaris when the major intracranial portion of the ramus superior of arteria stapedia atrophies ontogenetically. Such "secondary attachment" occurs in Pteropus (Chiroptera), Lagomorpha, Carnivora, ungulates, and many Rodentia.

Along the primate line only Lemuridae and Daubentoniidae retain the primitively complete superior ramus of arteria stapedia for life (Tandler, 1899; Hill, 1953b; Platzer, 1960). The definitive connection of the arteria meningea media, as found in man, was evidently a rather late phylogenetic development. As noted above, the orbital portion of the superior ramus of arteria stapedia generally persists in mammals. When the major part of the intracranial portion breaks down, secondary connections must be made. Along the primate line the ophthalmic artery tends to become the dominant stem for vessels of the orbit (Tandler, 1899).

In Nycticebus (slow loris) the ophthalmic artery sends off a recurrent branch re-entering the middle cranial fossa more laterally. This recurrent

branch then courses posterodorsally along the usual path of the middle meningeal artery (Davies, 1947). Obviously, this is the middle meningeal artery, which has retained rostral connection by way of its early anastomosis with the ophthalmic artery but has lost connection with its original stem; thus there is no attachment to the arteria maxillaris. A similar arrangement is found in Callithrix (Hapale) penicillata (marmoset), in which Tandler (1899) observed a recurrent branch from the lacrimal artery. (This only requires a shift within the orbit of the early anastomosis between the arteria stapedia and the arteria ophthalmica. The arteria lacrimalis may be a branch of either, depending on the species.) Why Davies (1947) thought the connection of the middle meningeal artery with the ophthalmic artery must represent persistence of the inferior ramus of arteria stapedia is difficult to understand; this is not the simplest explanation.

Hill (1953a) found no such recurrent artery in Tarsius. He did observe relatively large anterior meningeal branches of the ophthalmic artery. The arteria meningea media of Tarsius retains connection with its original stem, and thereby, with the arteria maxillaris, of which it is a definitive branch. It is enclosed by the roots of the auriculo-temporal nerve, as in man, but enters the cranial cavity through the foramen ovale. This raises a question as to its homology with the arteria meningea media of other Primates, especially in view of the observation that <u>Tarsius</u> has a conspicuously developed arteria stylomastoidea with an intracranial area of distribution corresponding with that of the usual arteria meningea media. Nothing comparable with this has been observed among mammals except in marsupials and edentates (Tandler, 1899; Hill, 1953a).

Although the proximal stem of arteria stapedia is larger in Lemuroidea than in Lorisoidea, it is generally (except in Lemuridae and Daubentoniidae) used up in supplying structures in the temporal bone, such as mucous membrane of the tympanic walls (Hill, 1953b).

In this respect the meningeal-artery pattern of monkeys, apes, and man seems closer to the pattern in <u>Nycticebus</u>. As a rule for monkeys and apes, there is still considerable inflow of blood from arteria ophthalmica into arteria meningea media, the proximal connection with the arteria maxillaris remaining quite weakly developed. In man the latter connection gains the ascendancy; yet the anastomosis with the arteria ophthalmica does typically persist, even if rather attenuated (Tandler, 1899; Wolff, 1954; de la Torre and Netsky, 1960).

Tandler (1899) postulated, on the basis of comparative anatomic observations, that the human arteria meningea media has been put together from a portion of the ramus inferior, a portion of the ramus superior, plus the meningeal ramification that usually springs from the ramus superior of the arteria stapedia. Based on studies of human embryos, Evans (1912) concluded that the proximal stem of the middle meningeal artery represents the remains of the common maxillo-mandibular stem of the stapedial artery. This would explain apparent secondary attachment to the maxillary artery.

As with most features of the cranial arterial system, these observations on the middle meningeal artery demonstrate that Tupaia is among the most primitive of all mammals: from its pattern could be derived that of Primates--or of Monotremata, Marsupialia, and all higher Eutheria.

Orbital Blood Supply (Relationship of the Internal and External Carotid Arteries)

The true arteria ophthalmica, as a branch of the intracranial portion of the arteria carotis interna, is a primary artery in vertebrates generally. In all vertebrate classes, this artery varies in degree of development (Tandler, 1899, 1901; Hofmann, 1900; Beddard, 1904b, 1905a, 1905b; Allen, 1905; Stephan, 1954).

In lizards the orbital contents are supplied by the true ophthalmic artery as well as by lacrimal and ophthalmic branches of the supraorbital and infraorbital (mandibular) divisions of the stapedial or facial carotid system derived from the extracranial stem of the internal carotid artery (Bhatia and Dayal, 1933; Burda, 1966).

In general among mammals there are three sources of arterial blood supplying orbital contents: (1) the arteria ophthalmica from the (intracranial) arteria carotis interna; (2) the orbital portion of the ramus superior of arteria stapedia from the (extracranial) arteria carotis interna; (3) the ramus orbitalis of arteria maxillaris (almost constantly from the arteria carotis externa in adults but derived from the extracranial inferior stapedial branch of the arteria carotis interna, embryologically). Any one of these three paths of inflow may be especially developed or degenerated. A complete continuum of possibilities can be demonstrated among mammals (Tandler, 1899).

In *Erinaceus europaeus* all three paths are supplied equally; similar relations are observed in

Lemur and *Daubentonia* (*Chiromys*) (Tandler, 1899).

Within a number of orders, certain forms show secondary reduction of the true arteria ophthalmica. In some Rodentia (e.g., *Lagostomus*), the arteria ophthalmica produces only an arteria centralis retinae (Beddard, 1904b). The arteria ophthalmica is rather weak in edentates and their allies (armadillo, sloth, ant-eater, pangolin), being nutritive to the bulbus oculi only. (Judging from its source, course, and embryological development, optic nerve and bulb appear to be this artery's primary distribution areas.) The arteria ophthalmica is not demonstrable in (virtually blind) *Talpa europaea* (Tandler, 1899). An arteria ophthalmica is retained, among Chiroptera, only in Pteropidae. In *Rhinolophus* (horseshoe bat) even the optic nerve artery may arise from the orbital ramus of arteria maxillaris (Grosser, 1901).

Thus, fairly well-developed ophthalmic arteries are found in prosimians, insectivores with normal vision, and in monotremes and marsupials generally. One can only speculate regarding the extreme reduction of these arteries in *Tupaia glis*. Assuming that other tupaiids are similar, one might suppose that the stapedial pathways, seemingly more directly in line with the main stem of the arteria carotis interna, would be more efficient than the more indirect intracranial branch. This view is also based on the assumption that, in the face of considerable expansion of the brain and eye, the vertebral arteries had not yet developed adequately, and the intracranial or cerebral carotid arteries had not readjusted appropriately. It would seem that Daubentonia and Lemur were even less adequate in this adjustment; here, however, the vertebral arteries have gained ascendancy to compensate for diminished cerebral carotid supply to the ophthalmic arteries. In all other Primates the adjustment was made at the expense of the stapedial system. Perhaps the development of a carotid canal was an important factor in this primate adjustment. Perhaps the detour of the stapedial stem through the stapes made one or the other less efficient. It is also of interest to note that the middle ear cavity of Tupaia is both relatively and absolutely larger than in man. In any event, the explanation for the reduced arteria ophthalmica is not directly apparent from the vessel relations. It may be noted that in Daubentonia and Lemur (with reduced arteria carotis cerebralis), the arteria ophthalmica arises at the point where the arteria carotis cerebralis bends posteriorly to give rise to the arteria communis posterior. This arrangement leaves the impression that the arteria communicans posterior gives off the arteria ophthalmica, and that the slender part of arteria carotis cerebralis also opens into the arteria ophthalmica (Tandler, 1899). It has been demonstrated, in Daubentonia and Lemur, that the widened portion of the arteria carotis cerebralis, between the arteria ophthalmica and the circulus arteriosus, actually carries blood in a reversed direction: out of the circulus arteriosus into the arteria ophthalmica (Platzer, 1960). In Tupaia glis the ophthalmic artery arises somewhat farther rostrally, from the anterior ramus of the arteria carotis cerebralis. In all prosimians, other than Daubentoniidae and Lemuridae, the arteria ophthalmica is the first branch of the arteria carotis cerebralis within the cranial cavity (Platzer, 1960).

In Tupaia glis the orbital contents are primarily supplied by supraorbital (superior ramus) branches of the arteria stapedia. The arteria ophthalmica probably supplies a small volume of blood to the ciliary branches. The arteria centralis retinae may arise from it or from a ciliary trunk. Such arrangements do vary among mammals (Rochon-Duvigneaud and Rode, 1943). Gross dissection could not reveal the source here. Although some bats completely lack an arteria centralis retinae (Grosser, 1901), the fundus photograph study of Samorajski, Ordy, and Keefe (1966) demonstrated that this artery is present in *Tupaia glis*. The ramus orbitalis of arteria maxillaris (infraorbital portion) appears to be practically excluded from orbital supply by its anastomosis with the ethmoidal branch of the ramus superior of arteria stapedia. The ramus orbitalis does send off a few small muscle branches, *en route* across the orbital floor.

The relative importance of infraorbital and supraorbital stapedial sources of supply to the orbit is quite variable among mammals. Monotremes have lost the major portion of the superior ramus of arteria stapedia, leaving the orbital ramification to be annexed by the arteria ophthalmica and the ramus orbitalis of arteria maxillaris (infraorbitalis). It is the latter source that evidently dominates in *Ornithorhynchus*, supplying all of the orbital contents except the bulbus oculi (Tandler, 1899). In *Echidna* rami ophthalmici of the arteria diploëtica magna (modified superior ramus of arteria stapedia) share in supplying soft parts (Tandler, 1899, 1901). In Marsupialia the pattern is described by Tandler (1899) as very similar to that in man; thus only a few weak branches extend to the inferior ocular muscles from the arteria maxillaris. No anastomosis with upper orbital vessels is demonstrable. The arteria ophthalmica is strong and has taken over the orbital ramification of the ramus superior arteriae stapediae. Edentates are rather variable in orbital supply from the three possible sources, with the well-developed ramus orbitalis of arteria maxillaris tending to take the lead. Microchiroptera (bats), while losing the arteria ophthalmica, vary in degree of dominance of the inferior or superior ramus of arteria stapedia. Although the superior ramus is primary, its main stem frequently drops out, and its orbital ramification persists to be annexed by the ramus orbitalis of arteria maxillaris (Tandler, 1899, 1901).

Thus, it is difficult to say whether the three-way balance observed in _Erinaceus_ is more primitive, or whether the balance favoring the ramus superior, as in _Tupaia_, is more primitive.

One may also ask whether the "ramus orbitalis" is primarily orbital or primarily ethmoidal in its distribution area. This, too, is difficult to determine from available evidence. Both supraorbital and infraorbital branches of the arteria stapedia typically send off ethmoidal branches, among lizards as well as mammals (Tandler, 1899, 1901; Hofmann, 1900; Bhatia and Dayal, 1933; Burda, 1966). An ethmoidal branch of the ramus superior may be observed extending into the nasal cavity of a mole embryo (nine millimeters in length). In a somewhat older embryo (thirteen millimeters in length), the extension of the arteria ophthalmica takes over the ramus orbitalis of arteria maxillaris. Later still, the arteria ophthalmica disappears completely (in an embryo seventeen and one-half millimeters in length) (Sicher, 1912). A similar sequential pattern occurs in bats (Grosser, 1901).

Among Prosimii, there is rapid embryological ascendance of the ophthalmic artery. In Daubentonia, this artery gives rise to two equal-sized branches in the orbit. The more superficial one anastomoses with the superior ramus of arteria stapedia. The united trunk sends off arteriae lacrimalis, frontalis, and ethmoidalis. The deeper branch of the ophthalmic trunk produces all of the arteriae ciliares (Tandler, 1899; Platzer, 1960).

Tandler (1899) observed no ramus orbitalis from the arteria maxillaris in Daubentonia. In Lemur, however, he did find a large ramus orbitalis joining the superior ramus, directly upon entry into the orbit. The main trunk of the ramus superior arteriae stapediae also communicates with the arteria ophthalmica before breaking up into the arteriae lacrimalis, frontalis, and ethmoidalis. The arteriae ciliares arise from the arteria ophthalmica itself.

Arctomys marmota (woodchuck), as a fairly primitive rodent, should be closer to the primate line than most other modern mammals. Here, the arteria stapedia has two well-developed rami. The superior ramus is the main source of blood to the orbit and eye. Within the orbit, it is joined by a well-developed anastomotic branch from the arteria carotis interna. This, according to Wolff (1938), closely resembles an embryonic stage in the origin of the ophthalmic artery in man. It also resembles *Daubentonia* and *Lemur*, as well as *Tupaia* and *Erinaceus*. However, in the adult *Tupaia*, the ophthalmic artery is reduced; in *Erinaceus*, the superior ramus is not dominant in supply of the orbit.

In *Loris*, *Galago*, and *Tarsius*, there is no ramus superior of arteria stapedia, as such. The arteria ophthalmica is well developed. There is, apparently, no longer a ramus orbitalis arising from arteria maxillaris. A few small muscle branches may represent it, in its reduced form (Tandler, 1899; Platzer, 1960).

This does not fully explain the loss of an ethmoidal branch of arteria maxillaris, still present in Tupaia. Barring the possibility of species and individual variability in the site of attachment of the ramus orbitalis with the ramus superior, it seems that loss of an ethmoidal branch of arteria maxillaris is a definite primate trend, one not observable in Tupaia glis or in most higher mammalian groups. It may also be noted that the "ethmoidal" extension of the intracranial anterior cerebral artery to the nasal septum, still prominent in Tupaia, regresses early in human embryos (Tandler, 1899, 1902). Reduction of the olfactory sense may be correlated with this. Such reduction is slight in Tupaiidae.

In monkeys, apes, and man, all orbital branches arise from the ophthalmic artery, with the exception of a few muscle branches from the arteria infraorbitalis to the inferior orbital region (Tandler, 1899; Lineback, 1933; Weinstein and Hedges, 1962).

The Circle of Willis (Relationship of the Vertebro-Basilar and Cerebral Carotid Systems)

In all inframammalian vertebrate classes the arteria carotis interna (as the arteria carotis cerebralis) alone supplies the brain. The arteriae vertebrales are rudimentary with respect to supply of the central nervous system. In all vertebrates the arteria carotis cerebralis terminates on the ventrolateral aspect of the brain, bifurcating into a ramus anterior (ramus cranialis) and a ramus posterior (ramus caudalis). The two rami posteriores unite as an arteria basilaris, continuing as an arteria spinalis ventralis (anterior) that diminishes in calibre caudally. Thus, although there is anastomotic connection between the vertebral and carotid arterial systems in all vertebrates, the former does not directly supply the brain in forms below mammals. Only in some reptiles (snakes) do lateral spinal arteries even penetrate into the cranial cavity in forming the basilar artery (Hofmann, 1900; de Vriese, 1905).

Comparative study of cerebral arteries alone will not establish an evolutionary scale. A similar disposition of arteries is to be found in groups phylogenetically far removed from one another. Within a single order (e.g., Rodentia) one finds patterns of the circulus arteriosus cerebri ranging from one extreme to another (Tandler, 1899; Hofmann, 1900; de Vriese, 1905).

Tandler (1899) distinguished three major types of arterial circle of Willis among mammals:

1. The internal carotid arteries supply the brain

more or less exclusively.

This arrangement is found in Monotremata and in kangaroos among Marsupialia. The pattern may be primary or secondary in Artiodactyla, Perissodactyla, Pinnipedia, Cetacea, and many Carnivora.

2. The vertebral and internal carotid arteries share, in varying proportions, in formation of the arterial circle.

Early vertebral artery development, along the mammalian line, led to appearance of this arrangement in some Marsupialia (opossum, e.g.) and in Insectivora generally. It is also found in some Chiroptera, some Rodentia (jerboa, rat), Lagomorpha, some Edentata (armadillo), as well as a number of Primates (some Lemuroidea and all Anthropoidea).

3. The internal carotid arteries are almost or completely excluded from involvement in the arterial circle, which is thereby formed by vertebral arteries alone.

Although obviously a secondary condition, this third arrangement appeared early in a number of primitive mammalian groups, including some Chiroptera, numerous Rodentia, some Edentata, and some Lemuroidea. This pattern has also been acquired by more highly evolved groups, such as some Carnivora.

The arrangement in <u>Erinaceus</u> and <u>Talpa</u> falls into the second category, above. The pattern resembles that of higher Primates in the slight development of the proximal stem (posterior communicating artery) of the posterior ramus of the cerebral carotid artery; thus the anterior cerebral and middle cerebral arteries appear to be mainly supplied by the anterior ramus, and the posterior cerebral arteries largely supplied by the bifurcation of the basilar artery (Tandler, 1899; Hofmann, 1900). The pattern observed in <u>Tupaia glis</u> (present study) closely resembles this insectivore pattern. Although the arteria communicans posterior is not small, its calibre is somewhat less than that of the anterior ramus or of the basilar branches of bifurcation and the stem of the posterior cerebral arteries arising from the latter. This observation conflicts with the published statements regarding the very reduced size of the arteria carotis interna after release of arteria stapedia in the tympanic region (Le Gros Clark, 1926a; Saban, 1956-1957). Although there are no published accounts of the arteria carotis cerebralis, it would presumably be small, as in Lemuroidea. In <u>Lemur</u> and <u>Daubentonia</u>, the arteria carotis cerebralis is attenuated and presumably supplies the arteria ophthalmica primarily. (See discussion of arteria ophthalmica, above.) The vertebral arteries and the basilar artery are well developed. The posterior communicating arteries are large, appearing as direct continuations of the branches of bifurcation of the basilar artery; thus the anterior, middle, and posterior cerebral arteries appear to be branches of these paired trunks (Tandler, 1899; Hill, 1953b; Platzer, 1960).

It seems that the reduction of the arteria promontorii (and of arteria carotis cerebralis) is a lemuroid specialization (Hill, 1953b; Lamberton, 1947). This condition probably occurs in some Tupaiidae (Le Gros Clark, 1926a; Saban, 1956-1957). The condition could have arisen, in parallel, in the two groups.

In other Prosimii (Lorisiformes and Tarsiiformes) the arteria promontorii is large. In *Loris* (*Stenops*) *gracilis*, the posterior communicating artery is described by Tandler (1899) as still quite large, much larger than in man. This most closely approximates the condition observed for *Tupaia glis* in the present study. *Tarsius* shows greater reduction of the posterior communicating arteries (Hill, 1953a).

It appears that both Tupaiidae and prosimians reached a critical phase in achieving balance between the ascending vertebro-basilar system and the well-established internal carotid system that was just keeping up with it in the supply of the rapidly expanding brain. Two divergent paths may have followed, perhaps in parallel. Along one path, leading to higher Primates, the internal carotid system maintained an important role. Along another path (not necessarily a single ancestral line) leading to Lemuridae, Daubentoniidae, and some <u>Tupaia</u> species or individuals, the vertebro-basilar system gained the ascendancy. Perhaps the progressive accentuation of the bending of the telencephalon (related to its great development) played a role in the recovery of the importance of the internal carotid system. Decérisy (1952) observed (by study of corrosion preparations) that as one progresses from lemuroids to anthropoids the circle of Willis gradually abandons its plane aspect to achieve a progressive folding of two half-rings that tend to close in the manner of pages in a book.

In Chiroptera and Rodentia the circle of Willis varies in relation to the degree of atrophy of the internal carotid artery; in the majority the vertebral system outweighs the internal carotid system (Grosser, 1901; de Vriese, 1905).

The Circle of Willis (Nature of the Posterior Region)

The posterior region of the circulus arteriosus cerebri of *Tupaia glis* appears to be more primitive than in *Erinaceus* and *Talpa*. A few features resemble those of certain prosimians. The greatest similarity is to such forms as *Macropus* (kangaroo), *Myrmecophaga jubata* (giant ant-eater) and *Echidna* (spiny ant-eater). Adequate comparisons cannot be made. Tandler's descriptions (1899, 1901) and those of most primatologists are limited to the proportions of the circle of Willis itself, without description of all branches and their distribution. Hofmann's descriptions (1900), although detailed, do not include monotremes, marsupials, or primates. Abbie's detailed descriptions (1933, 1934) of certain arteries of the brain do not include any prosimians or insectivores. No definite conclusions can be drawn from the few observations to be cited here.

The bifurcation of the basilar artery into a common trunk, on each side, for the superior cerebellar and posterior cerebral arteries is a feature shared by *Tupaia glis* with *Myrmecophaga jubata* (illustration closely resembling asymmetrical tree shrew 3), *Macropus* (Shellshear, 1930), *Dasypus novemcinctus* (Hofmann, 1900), and certain prosimians. Such common trunks (two millimeters in length) were described by Beddard (1904a) for *Perodicticus potto*. Tandler (1899) stated that the two large posterior communicating arteries of *Daubentonia* (*Chiromys*) *madagascariensis* arise from the basilar artery. Each then sends off the arteria cerebelli superior and the arteria cerebri posterior as side branches. The description for *Lemur varius* was much the same.

In *Erinaceus europaeus* and *Talpa europaea*, the pair of arteriae cerebelli superiores arise at the bifurcation of the basilar artery into the stems of the posterior cerebral arteries (Hofmann, 1900). This arrangement was observed unilaterally in one specimen of *Tupaia glis* (present study).

The presence of a truncus communis, as observed in the limited sampling of marsupials, edentates, prosimians, and tupaias, would seem to be the result of incomplete fusion of the arteria basilaris elements, embryologically. Various forms of incomplete fusion, including island formation, are common in reptiles and primitive mammals (Hofmann, 1900; de Vriese, 1905, Shindo, 1914).

The presence of a few branches representing "posterior cerebral" elements, in Tupaia glis, is clearly a primitive mammalian feature.

In Reptilia, the posterior cerebral artery still arises from the anterior ramus of the arteria carotis cerebri (Hofmann, 1900; Shindo, 1914; Abbie, 1934). In general among Mammalia the posterior cerebral artery or arteries tend to arise more and more posteriorly, along primate and other evolutionary lines. These successively more posterior positions have been designated as alpha, beta, gamma, and delta, by Hofmann (1900). The dorso-posterior extension of each cerebral hemisphere shifts the major field of supply posteriorly; thus the stem shifts to the nearest source of supply. This source is the stem of the longitudinal anastomotic channel extending from the arteria basilaris to the arteria carotis cerebralis on each side. In man the posterior cerebral artery has reached its ultimate posterior stem of origin (Hofmann's "arteria cerebralis posterior delta"). Since the area of supply lies almost directly above the midbrain, it utilizes mesencephalic vessels, exclusively, as a source of blood (Abbie, 1934). Shellshear (1930) postulated that "in the Mammalia the invasion of the cerebral hemispheres by visual, tactile, and auditory tracts from the midbrain and thalamus would seem to have had the effect of grouping together the metameric branches to the corpora quadrigemina, the geniculate bodies and the thalamus."

In Echidna, Shellshear (1930) saw branches arranged in parallel series for distribution to corpora quadrigemina and the lateral aspect of the midbrain. He described (1930) a similar array of metameric branches from a longitudinal channel in Myrmecophaga jubata.

Tupaia glis is somewhat less metameric; several, fairly parallel branches share a common stem from the posterior communicating artery (longitudinal channel from the basilar artery to the internal carotid artery).

The mesencephalic artery of Tupaia glis may correspond with the "arteriae cerebri posteriores gamma and delta" of Hofmann (1900). It may be considered as, in some degree, "cerebral" in distribution: it supplies the splenium region of the corpus callosum and forms anastomoses with branches of cortical distribution. The artery here described (for Tupaia glis) as the arteria cerebri posterior may represent the "arteria cerebri posterior beta" of Hofmann (1900). The arteria choroidea anterior of Tupaia glis would correspond, in source and in part of its distribution, to Hofmann's (1900) "arteria cerebri posterior alpha"; however, this artery appears to have no cerebral distribution in *Tupaia glis*.

In view of the greater cerebral development of *Tupaia*, it seems strange that this animal would show less fusion of branches than is observed in *Erinaceus* (Hofmann, 1900); the anterior colliculi of *Tupaia* do remain almost reptilian in relative size, however. More thorough tracing of branches, in serial sections of the brains of representative primitive groups, will be required to make adequate comparisons.

The Circle of Willis (Mode of Anterior Closure)

The mode of anterior closure of the circulus arteriosus cerebri is of some phylogenetic interest.

In *Tupaia glis* the two arteriae cerebri anteriores (terminations of the anterior rami of arteriae carotis cerebralis) are interconnected, anterior to the optic chiasma, by a transverse arteria communicans anterior. From this, in turn, a median, initially unpaired arteria cerebri anterior communis extends posteriorly to bifurcate again about half of the distance backward over the corpus callosum.

Although Tandler (1899) used the term

"arteria communicans anterior" in his description of *Erinaceus europaeus* and *Talpa europaea*, the account of the vessel is too brief to be sure of its nature, other than that it closes the circle anteriorly. Hofmann's (1900) detailed description of these two insectivore species indicates differences from *Tupaia glis*. He stated that the anterior ramus of each arteria carotis cerebralis converges toward its counterpart as it courses anteriorly within the longitudinal fissure anterior to the optic chiasma. The two arteries there unite as an unpaired arteria cerebri anterior communis; thus there would be no anastomotic arteria communicans anterior. The arteria cerebri anterior communis then gives off a large arteria bulbi olfactorii medialis, distributed primarily to the medial surfaces of the olfactory tracts and bulbs. The arteria cerebri anterior communis bifurcates into the arteriae corporis callosi in this olfactory region. The arteriae corporis callosi then bend backward and ramify on the upper surface of the corpus callosum, as in *Tupaia glis*.

Tandler's (1899) descriptions of *Lemur varius*, *Daubentonia* (*Chiromys*) *madagascariensis*, *Loris* (*Stenops*) *gracilis*, and *Galago* (*Otolicnus*) *crassicaudatus* indicate presence of a median artery that arises by merging of the anterior cerebral arteries. For Lemur and Daubentonia he indicated that each anterior cerebral artery sends a branch forward to supply the bulbus olfactorius. Regarding Simiae, Tandler (1899) mentioned that the unpaired median continuation of the anterior cerebral fusion winds around the genu of the corpus callosum and bifurcates distally. For man, he stated that the anterior cerebral arteries are united by an anterior communicating artery.

Beddard's (1904a) description of Perodicticus potto indicated formation of an unpaired arteria corporis callosi before turning upward over the surface of the corpus callosum. He stated that no arteria communicans anterior is present; union was described as oblique. The arteria corporis callosi divides again, farther posteriorly, above the corpus callosum.

Lemur macaco and Lemur coronatus were both described by Beddard (1904a) as possessing a stout anterior communicating artery, from which arises the briefly single anterior cerebral artery. After a very short course over the corpus callosum, paired anterior cerebral arteries (arteriae corporis callosi) are formed again. Of all descriptions found in the literature, this most closely corresponds with that in Tupaia glis.

Similar variability in union of the anterior cerebral arteries occurs in other orders, such as Rodentia and Artiodactyla, as well as in the class Reptilia (Tandler, 1899; Hofmann, 1900; Beddard, 1905b; de Vriese, 1905; Shindo, 1914; Abbie, 1934; Burda, 1966).

De Vriese (1907) concluded that, within the vertebrate series, the anterior cerebral arteries show three major patterns:

1. The two anterior cerebral arteries run parallel, with no connection between them. This most primitive arrangement is found in fishes, some amphibians, some reptiles, and all birds.
2. The two anterior cerebral arteries are interconnected by one or more anterior communicating arteries in front of the optic chiasma; beyond this, the two run parallel again. This pattern occurs in some amphibians and some mammals.
3. The two anterior cerebral arteries converge, anterior to the optic chiasma, to form an unpaired arteria cerebralis anterior communis (arteria corporis callosi, in some cases), which dissociates again, after a varying distance, into two branches. This arrangement is the common one, being found in most reptiles and most mammals.

De Vriese (1907) observed the embryological sequence, as found in an animal (rabbit) with the third arrangement described above. Initially, the arteriae cerebrales anteriores lie parallel to each other; then these two arteries become interconnected by a transverse vascular network; subsequently the two anterior cerebral arteries become connected by an arteria communicans anterior. Extending anteriorly from this anastomosis are one deep, and two superficial, median anterior cerebral arteries. In the final developmental phase, the two anterior cerebral arteries merge as an unpaired stem, due to atrophy of one of the primitive superficial anterior cerebral arteries and the deep median anterior cerebral artery anterior to the level of the anterior communicating artery, which is also lost.

Tupaia glis appears to have reached a stage between the third and fourth, as described above. Man's development appears to have stopped at the third stage, with some loss of branches. Barring secondary regression, _Tupaia_ seems more primitive in this respect than modern insectivores and most prosimians.

The Arteries of the Olfactory Region

The literature reveals the primitive nature of the collaterals that the terminal anterior ramus of arteria carotis cerebralis sends to the olfactory lobe. Names and descriptions are so varied as to make comparison difficult. There is little doubt that the anterior ramus of the arteria carotis cerebralis primitively passes through the lamina cribrosa, from the medial surface of the olfactory lobe, to terminate in the septum narium. The arteriae bulbi olfactorii of *Tupaia glis* retain this condition, also described for *Vespertilio* and *Vesperugo* species among bats (Grosser, 1901). The intracranial arteria carotis interna is therefore the artery of the frontal process as well as the brain.

Hofmann (1900) described the large anterior continuation of the anterior ramus of arteria carotis cerebralis, in *Erinaceus* and *Talpa*, as the arteria bulbi olfactorii medialis. Although most of the branches of this vessel, in *Tupaia*, are concentrated medially, some also extend to the lateral surface.

Tupaia, like *Erinaceus* and *Talpa*, has a ramus ethmoidalis (arteria bulbi olfactorii lateralis) given off by the arteria cerebri anterior, shortly after exit of arteria cerebri media. This ramus ethmoidalis courses craniad to end in a rete ethmoidale lying within the dura on the lamina cribrosa of the ethmoid bone. In *Tupaia* the ethmoidal branch of the superior ramus of arteria stapedia joins the ramus ethmoidalis in the dura mater covering the olfactory lobe. Hofmann (1900) described a connection of the rete ethmoidale with vessels of the orbit, through a foramen ethmoidale, in *Erinaceus* and *Talpa*. The rete ethmoidale sends numerous small twigs into the nasal cavity with the fila olfactoria in all three genera (*Tupaia*, *Erinaceus*, and *Talpa*). This pattern of ethmoidal branches is probably primitive. A description of these vessels in Crocodilia is quite similar (Beddard, 1905b).

The anterior ethmoidal artery of man is evidently the homologue of the orbital ethmoidal ramus (Wolff, 1954; de la Torre and Netsky, 1960). The literature does not reveal the level of primate phylogeny at which the extension of the arteria cerebri anterior to the nasal septum underwent regression.

CONCLUSIONS

The primitive mammalian features observable in the branching pattern and distribution of the cranial arteries of *Tupaia glis* include the following:

1. The branching pattern of the arch of the aorta is nearly symmetrical.
2. The lingual artery is still the major branch of the external carotid stem. The facial and superficial temporal arteries are rather slender vessels.
3. The superior ramus of arteria stapedia is well developed, retaining continuity with its meningeal and orbital ramifications.
4. The pterygoid portion of the arteria maxillaris passes through an external alisphenoid canal.
5. The ethmoidal rami of the arteria infraorbitalis, arteria supraorbitalis, and arteria carotis cerebralis all remain well developed, with that of the arteria cerebralis anterior still terminating on the nasal septum.
6. The promontory and stapedial arteries have remained about equal, both being of considerable diameter. (The literature contains conflicting observations of this feature, however.)

7. An anterior communicating artery is formed between the anterior cerebral arteries. The formation of a common anterior cerebral artery, beyond this point, is also quite primitive.

8. Well-developed arteriae bulbi olfactorii appear as continuations of the anterior cerebral arteries themselves.

9. The superior cerebellar arteries arise from the branches of bifurcation of the basilar artery.

10. There is a fairly segmental arrangement of origins of the posterior cerebral artery components, with mesencephalic arteries arising directly, and independently, from the posterior communicating artery.

Features of the cranial arteries of *Tupaia glis* that show some similarity to the Primates are the following:

1. There is a trend toward concentration of aortic arch branches and shifting of their origins toward the (right) brachiocephalic trunk.
2. There is reduction and possible loss of the proximal inferior ramus of the stapedial artery.
3. The orbital ramus of the arteria infraorbitalis may no longer be significant in supply of orbital contents.
4. The internal carotid artery and its branches course through bony canals in the medial wall of

the tympanic cavity.

5. The vertebro-basilar arterial system appears to contribute to the circulus arteriosus cerebri about equally with the internal carotid arterial system. (On this point, there is some implied disagreement in the literature.)

All of the features listed above, with the possible exception of the third, have also appeared along other mammalian lines of evolution; thus they may also have arisen independently here. There is good fossil evidence for this, in the case of the fourth feature. There is no convincing evidence favoring direct derivation of primates from a tupaioid stock; it does remain a possibility since no features preclude such ancestry.

Since lipotyphlan ancestors and leptictids are more tupaiid-like in dentition in the Eocene than in the Oligocene epoch, and since early leptictids are often difficult to distinguish from primitive marsupials (van Valen, 1965), tupaioid forms probably arose in Cretaceous or Paleocene times. In many features, including cranial arteries, a tree shrew is as primitive as any mammal. The numerous features in which tree shrews resemble marsupials also are indicative of great antiquity. Tree-shrew-like animals may have appeared close to the time of eutherian-metatherian divergence in the late Cretaceous period.

Although primitive mammalian features are numerous, a few are indicated below:

1. There is a high proportion of acrocentric chromosomes.
2. Tufts of hair are associated with scales on the tail (*Ptilocercus*).
3. Seven or eight well-developed palatine ridges are present.
4. Lytta and sublingua are both present in the tongue.
5. The entire length of the intestine is freely suspended by a median dorsal mesentery.
6. The large intestine is a short, wide, straight tube, undifferentiated into colon and rectum (*Ptilocercus*, *Dendrogale*, and some *Tupaia* species).
7. Paired precavae are present in the venous system.
8. The branching pattern of the internal carotid arterial system closely resembles that of all mammalian embryos at an early post-branchial stage.
9. The suprarenal cortex lacks a zona reticularis.
10. Harder's glands are well developed.
11. The nictitating membrane is fairly well developed.
12. Most optic nerve fibers cross at the optic chiasma.

13. The anterior colliculi remain relatively very large.
14. Amniogenesis involves folding.
15. The allantois is a very large, folded vesicle.
16. The yolk sac is well developed.
17. A pubo-ischial symphysis is present.
18. The embryonic skeleton of the hand and foot is similar to that of lower tetrapods. Four centralia are present in carpus and tarsus.

Seemingly close affinity of tupaiids to marsupials is indicated by the following features:

1. The branching of the aortic arch is fairly symmetrical.
2. There is a single (left) azygos vein, commonly.
3. The sublingua is retained.
4. The facial complement of vibrissae is almost complete.
5. The corticospinal tract courses in the dorsal funiculus of the upper spinal cord only, with fibers terminating in the dorsal or intermediate gray column.
6. The testes remain anterior to the penis.
7. Each testis is enclosed in a separate cremaster sac. Descent into the scrotum is generally permanent.
8. There is extracranial passage of the inferior petrosal (venous) sinus.

9. The vomeronasal supporting cartilages are quite similar.
10. Palatal vacuities are generally present (absent in <u>Dendrogale</u>).
11. A tympanic wing of the alisphenoid bone is present and shows a posterior concavity.
12. An external alisphenoid canal is commonly present.
13. The combination of an enclosed orbit and a wide-angle optic axis is present in some members of both groups.
14. The tritubercular molar teeth of <u>Adapisoriculus</u> and Recent tupaiids show similarity to those of primitive marsupials.
15. Capitate and hamate bones, together, are larger than navicular and lunate bones combined.
16. There is broad confluence of the sustentacular facet with the navicular facet of the talus.
17. A choriovitelline placenta is present during the early gestation period.

Features of Tupaiidae that are primitive for Eutheria include the following:

1. The annulus tympanicus lies free within the tympanic cavity.
2. The corpus uteri is very short.
3. The depth of implantation of the embryo is

superficial; no decidua capsularis is present.

4. The endometrial glands remain functionally active in the pregnant uterus.

5. A choriovitelline placenta persists during an early stage of gestation.

The very substantial number of similarities, whether parallelisms or not, between tupaiids and primates seems to indicate a rather proximate common ancestor, possibly in leptictid stock. Many of these similarities are adaptations to an arboreal habitat or may be the indirect fruits of that adaptation. Some of these traits can be regarded as probable parallelisms on the basis of available paleontological evidence; yet there are different evolutionary routes to an arboreal way of life, as indicated by squirrels and phalangers. There must have been a large number of genes and chromosomes with similar dispositions for change in the early tupaiid and primate stocks. Features of Tupaiidae that do not seem highly correlated with arboreal habits and that appear to have a common genetic basis with Primates are the following:

1. There is a characteristic pattern of friction ridges of the volar integument.

2. A pendulous penis is found in both groups.

3. There is retention of the combination of lytta

and sublingua.

4. Incipient demarcation exists between a transverse and a descending colon (Tupaia).

5. A vascular mesotyphlon is present.

6. The ratio of corneal to scleral diameter falls within the same range, unique among mammals.

7. A free annulus tympanicus is retained.

8. There is development of a hypoconulid on the last molar tooth (Ptilocercus).

9. A mesostyle is present on the molar tooth (Tupaia).

10. Musculus digastricus has a well-developed central tendon (Tupaia).

11. The naso-labial facial musculature extends into the median frontal region.

12. Superficial orbito-auriculo-labial musculature is present.

13. The internal oblique aponeurosis lies dorsal to musculus rectus abdominis in its anterior portion and lies ventral to musculus rectus abdominis in its caudal portion.

14. A pyriformis muscle is present.

15. There is early synostosis of the fissure of Glaser.

16. There is reduction and possible loss (partial or complete) of the proximal inferior ramus of

arteria stapedia.

17. Cytoarchitectural patterns of the cerebral cortex are similar.

18. Immunochemical correspondence of serum albumins is within the prosimian range.

19. Proteins in tupaiid lenses are more similar to those of primates than to any non-primates.

It seems evident that special resemblances to lemurs, as opposed to other prosimians and primates generally, are especially suspect as possible parallelisms.

It is the conclusion of the writer, based on the survey of the literature and the observation of the cranial arteries, that the current evaluation of the phylogenetic position of Tupaiidae by many paleontologists (Romer, 1966) is the most plausible; hence Tupaiidae are representative of a very primitive eutherian insectivore stock. This stock is presently designated as the suborder Proteutheria of the order Insectivora. It must be emphasized that the order Insectivora is an exceedingly broad category including all eutherian stem forms. Szalay (1968) has indicated that many paleontologists currently tend to utilize the Insectivora as a catch-all category pending adequate fossil evidence. Until such evidence is available it does seem unwarranted, however, to set up a separate order Tupaioidea, as suggested by Straus (1949) and by Martin (1966).

SUMMARY

Based on evidence from a study of the internal carotid arterial system and a survey of the literature on tupaiid affinities, it is concluded that the family Tupaiidae remains fairly representative of an ancestral stock of insectivores diverging from metatherian stock in late Cretaceous times. Superimposed upon this fundamentally primitive condition are numerous arboreal adaptations and sequelae that closely resemble those found in some Prosimii. Many of these similarities have an apparent genetic basis; thus they have probably arisen by parallelism from a common stock possessing numerous genes with similar potentialities for change.

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