THE COMPARATIVE ANATOMY OF THE CEREBELLUM OF THE LESSER BUSH BABY (GALAGO SENEGALENSIS) AND THE TREE SHREW (TUPAIA GLIS)

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This is to certify that the

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THE COMPARATIVE ANATOMY OF THE CEREBELLUM OF THE LESSER BUSH BABY (Galago Senegalensis) AND THE TREE SHREW (Tupaia Glis)

presented by

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has been accepted towards fulfillment
of the requirements for

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ABSTRACT

THE COMPARATIVE ANATOMY OF THE CEREBELLUM
OF THE LESSER BUSH BABY *(GALAGO SENEGALENSIS)*
AND THE TREE SHREW *(TUPAIA GLIS)*

by Duane E. Haines

The prosimians are in a key phylogenetic gap between the insectivores and the higher primates, and represent an important group of animals to the anthropologist and neuroanatomist. To the anthropologist the prosimians represent the group of animals from which primate characteristics, both morphologic and behavioral, first emanate. To the neuroanatomist the prosimians, as a group, represent the point from which certain neurological regions become more complex, while other regions undergo regression in the course of primate phylogeny.

The cerebellum of prosimian primates has received little attention. It has been only briefly discussed in the course of studies on other portions of the prosimian central nervous system (Elliot Smith, 1903a; Le Gros Clark, 1924, 1926, 1931; Woollard, 1925; Tilney, 1927; Kanagasuntheram and Mahran, 1960; Krishnamurti, 1966).

Van Valen (1965) and Campbell (1966a, 1966b) have reviewed the differing opinions on the classification of *Tupaia* and concluded that a close *Tupaia*-primate relationship is possibly difficult to establish.

The purpose of this study was to describe the gross and microscopic anatomy of the cerebelli of the *Galago* and *Tupaia*. An addi-

tional purpose was to provide information relevant to the "total morphological picture" of *Tupaia*, and to discuss the phylogenetic implications of the morphology of the *Tupaia* cerebellum.

The anterior lobe of the cerebellum of *Tupaia* is composed only of a vermal portion, while in *Galago* large lateral portions of the culmen and central lobule are present. It is possible that the larger paraflocculus of *Tupaia* helps to compensate for the limited development of the anterior lobe.

The ansiform lobule of *Tupaia* is made up of 4 - 5 folia compared to 2 folia in the *Galago*. The remaining portions of the hemisphere are mainly composed of the paramedian lobule which has 4 folia in both *Galago* and *Tupaia*. The copula pyramidis is vertically fissured in *Tupaia* and horizontally fissured in *Galago*. This has been interpreted as a progressive phylogenetic development.

The cytoarchitecture of the cerebellar cortex of the *Galago* and *Tupaia* does not differ significantly from the *Macaca* (Fox *et al.*, 1967).

The treeshrew *(Tupaia)* and the lesser bushbaby *(Galago)* have three cerebellar nuclei on each side, a medial or fastigii, an interpositus, and a lateral or dentate. The medial cerebellar nucleus is separated from the interpositus nucleus by coarse bundles of fibers intermixed with large multipolar neurons. The interpositus and lateral nuclei are incompletely separated from each other throughout their rostro-caudal length. The lateral nucleus of the *Galago* has irregularities in its boundaries that give it the appearance of

primitive laminations. These laminations are less apparent in *Tupaia*. All cerebellar nuclei in both animals are composed on small (14-24 micra) to medium (25-30 micra) sized multipolar neurons.

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by

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INTRODUCTION

An understanding of the function of a part must be preceded by a complete understanding of the morphology of the part. Comparative neuroanatomical studies provide important information on structures and systems of structures that have either become more complex or undergone regression in the evolution of higher primates and man. A broad understanding of a wide range of animals is necessary when attempting to trace phylogenetically the development or regression of a structure or system. In the nervous system comparative studies provide a great deal of information relative to similar systems in higher and lower forms. The prosimian primates are at a key phylogenetic position not only from the anthropologist's point of view, but also from the neuroanatomist's standpoint. To the anthropologist the prosimian represents the link from insectivores to higher primates and man. To the neuroanatomist the prosimians represent that point from which certain regions begin to evolve (e.g., cerebral cortex) and certain other regions become less important to the function of the organism (e.g., olfactory system). Since the preliminary studies of Elliot-Smith (1903a), Le Gros Clark (1924, 1926, 1931), Woollard (1925) and Tilney (1927) very little attention has been focused on the cerebellum of prosimian primates. It is the goal of this study to provide a substantial foundation for future studies on the prosimian cerebellum by precisely defining the gross and microscopic anatomy of the cerebelli of the two prosimian primates, *Galago* and *Tupaia*.

A second and by no means minor fact of consideration is the author's interest in physical anthropology and evolution. One of the animals used in this study *(Tupaia)* has received a great deal of attention concerning its phylogenetic classification. The question is, simply stated, whether it should be classified as an Insectivore or a Prosimian. This study does not propose to answer this question in its entirety, but to provide more detailed information to aid in a clearer understanding of the "total morphological picture" as its importance is stressed by Le Gros Clark (1959). This study centers on the comparative anatomy of the cerebelli of *Tupaia glis*, a low prosimian, and *Galago senegalensis*, a more advanced prosimian. Comparative studies on the nervous system contribute a great deal to current anthropological problems, as pointed out by Holloway (1968).

> "Two aspects of neurology have particular significance for the anthropologist's area of study: palaeoneurology and comparative neurology. The former studies the changes as they appear in the fossil record, while the latter attempts to better understand the nature of extant forms through study of structure and function."

Animals of the type used in this study, though not rare, are difficult to obtain. A colony of *Galago senegalensis* was established in the Anatomy Department in 1967 (Holmes *et al.*, 1968), and animals from this colony were used in the present study. The cerebellum was chosen because of its relationship to agility and behavior and the phylogenetic implications of this relationship in prosimians (Stephan and Andy 1964), and because of the voids in the literature on the details of the prosimian cerebellum. The early investigators

previously mentioned, and recent investigators, deal with the prosimian cerebellum only in passing.

With the current trend to use small primates in the laboratory, precise data on basic anatomy are surely needed. Without this basic anatomical information more advanced studies cannot be initiated, or if they are, the relative lack of information imposes an ever present obstacle. The author does not consider this study an end in itself, but hopes it provides substantial foundation for future anatomical, physiological and anthropological studies on the prosimian cerebellum, and indeed the entire prosimian brain stem. The potential that a small primate possesses for the medical researcher, and the importance of the prosimians to the anthropologist, warrant clear descriptions and definitions of basic anatomical parameters.

CLASSIFICATION

All living primates are grouped into two large suborders, the *Prosimii* and the *Anthropoidea*. This present study deals with members of the suborder *Prosimii*, and incorporates a borderline prosimian, the tree shrew, and a more advanced prosimian, the lesser bushbaby.

The suborder *Prosimii* is further subdivided into six families that span the gap in the evolution of primate morphology between the insectivores and Simians (Buettner-Janusch 1966; Napier and Napier 1967). These families are the *Tupaiidae*, *Lemuridae*, *Indriidae*, *Daubentoniidae*, *Lorsidae* and *Tarsiidae*, in respective order from insectivores to primates (Fig. 1).

GALAGO SENEGALENSIS

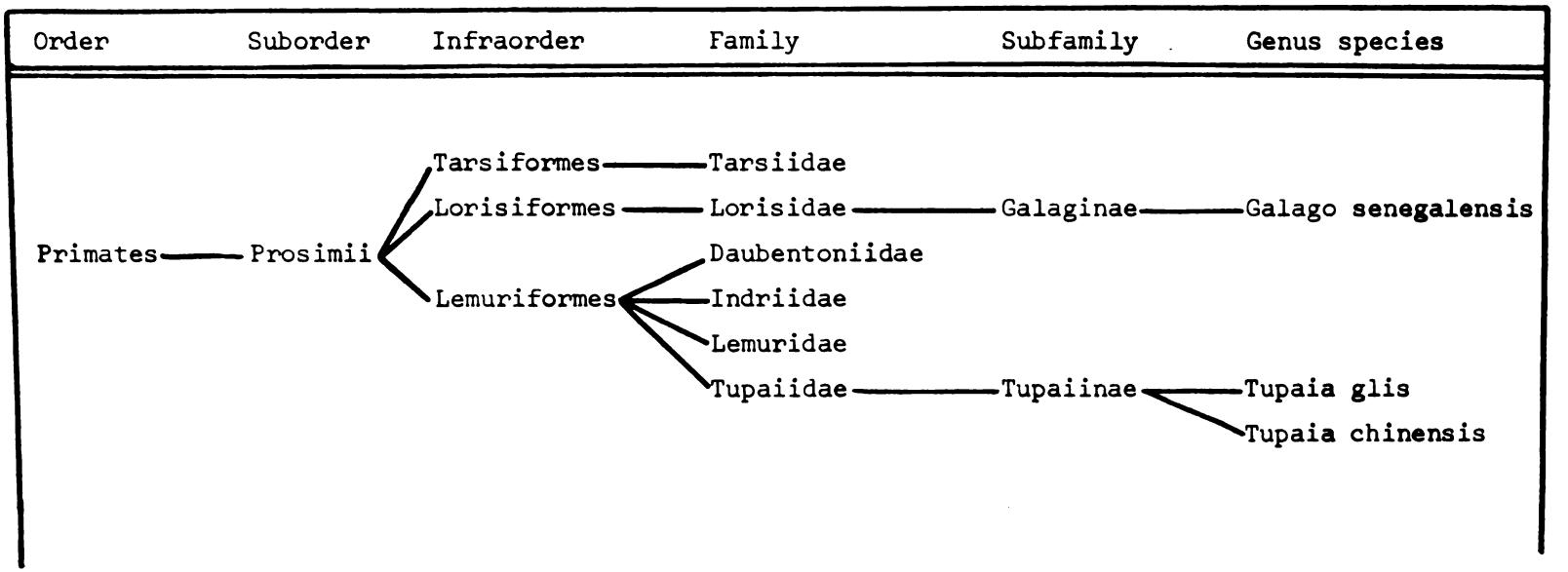
The lesser bushbaby *(Galago senegalensis)* is a member of the family *Lorisidae*, therefore represents a more advanced prosimian. The complete classification of *Galago* is as follows (Fig. 1):

Order	Primates
Suborder	Prosimii
Infraorder	Lorisiformes
Subfamily	Galaginae
Genus	*Galago*
Species	*Senegalensis*

TUPAIA GLIS

The tree shrew *(Tupaia glis)* is a member of the family *Tupaiidae*. The relative phylogenetic position of *Tupaia* has been investigated by numerous anatomists and anthropologists and even to date opinion differs. Van Valen (1965) reviewed early and recent literature and comes to this conclusion:

Fig. 1 Schematic classification of the prosimians used in the present study.



> "I believe the better course...is to refer the Tupaiidae to the Insectivora without taxonomically expressing a special relationship to any of the other groups of insectivores."

Campbell (1966a, 1966b) re-evaluated the evidence of the nervous systems and also concludes that a close tupaiid-primate relationship is difficult to establish. It is significant to note, however, that all recent studies on the tupaiid nervous system have been restricted to the pyramidal tract (Jane *et al.*, 1965; Campbell, 1965; Verhaart 1966), or to observation on the visual system (Tigges, 1964, 1966; Tigges *et al.*, 1967; Campbell *et al.*, 1966; Glickstein *et al.*, 1966; Glickstein, 1967; Snyder and Diamond, 1968). It does not seem valid to definitively suggest a phylogenetic position for *Tupaia* based on discrepencies in two neurological systems. There are other systems just as important as these, and this position is open for challenge. Stephan and Andy (1964) briefly commented on the "larger cerebellum (in *Tupaia*) than either of the monkeys, *Callithrix* and *Leontocoebus*." They further state that the size of the *Galago* cerebellum may be related to the "marked agility" of the lesser bushbaby. In this present study the cortical topography of the cerebellum of *Tupaia* is just as complex as that of *Galago*, even though the latter cerebellum is slightly larger. If the suggestion of Stephan and Andy (1964) is partially true, the complexity of the *Tupaia* cerebellum should be explained, since this animal is not necessarily noted for its agility.

In view of varying opinions concerning *Tupaia* classification, this author has consulted the evaluations of recent authorities

(Le Gros Clark, 1959; Buettner-Janusch, 1963, 1966). Since an animal is classified on the basis of all its morphological characteristics and affinities for a particular family, Le Gros Clark (1959) has stated for *Tupaia:*

> "...they show in their total morphological pattern such a remarkable number of intimate resemblances to the lemurs, and particularly the Lemuriformes, that their affinities with the latter can no longer be doubted."

The tree shrew *(Tupaia glis)* is undoubtedly a primitive primate, but classified as a primate (Buettner-Janusch, 1963; Napier and Napier, 1967). The full schema of *Tupaia* classification is as follows (Fig. 1):

Order	Primates
Suborder	Prosimii
Infraorder	Lemuriformes
Family	Tupaioidea
Subfamily	Tupaiinae
Genus	*Tupaia*
species	*glis & chinensis*

REVIEW OF THE LITERATURE

GENERAL REMARKS

The cerebellum, as a general subject, has received varied amounts of attention depending on the animal or group of animals under consideration (Ariens Kappers *et al.*, 1936). In the first part of a comprehensive work on the comparative anatomy of the cerebellum Larsell and Jansen (1967) studied vertebrate animals covering the phylogenetic scale from hagfish and lampreys to birds. A large amount of information has been published on the cerebelli of higher mammals and man. The animals most commonly used in physiologic studies on the cerebellum are cats and various simian primates (Eccles *et al.*, 1967). Therefore, a great deal of recent information is available for the cat (Snider, 1940; Larsell, 1953; Flood and Jansen, 1961; and others) and for various simian primates (Braitenberg and Atwood, 1958; Voogd, 1967; Mussen, 1967; and others). These studies will not be reviewed since these animals possess cerebelli that are considerably more complex than the prosimian cerebellum, cats are not primates, and a review of these studies would not contribute to the present study.

Future reference to the cerebelli of more advanced forms, e.g., cat and simian, will be utilized only when it helps to clarify a point.

CEREBELLAR CORTEX-TOPOGRAPHY

A thorough review of the literature has revealed very little available information on the detailed morphology of the prosimian

cerebellum. The early studies of Le Gros Clark (1924, 1926, 1931), Elliot Smith (1903a), Woollard (1925) and Tilney (1927) have been followed by the recent observations of Kanagasuntheram and Mahran (1960) and Krishnamurti (1966). In all of these cases the cerebellum was not the primary topic of discussion and consequently received a parcity of attention. In the following review only those articles on the prosimian nervous system will be considered. Other animals with a morphologically simple cerebellum (e.g., rat, small marsupials monotremes, avian, etc.) will be included only when they clarify and/or compliment a particular point of the discussion.

Elliot Smith (1899b) in an early study on the brains of sloths and anteaters noted that the terminology used in human anatomy to describe the morphology of the cerebellum is ill-adapted to comparative observations, particularly when dealing with cerebelli of simple organization. In a later study of the lemur brain, Elliot Smith (1903a) proposed a schema based on the recognition of a "preclival" fissure. This fissure is the deepest fissure crossing the mesial line, and is universally present in all mammals (Elliot Smith, 1903a). Using this fissure as a landmark Elliot Smith (1903a) designated three main lobes: The anterior lobe (rostral to the primary fissure - a term synomous with "preclival"), the middle lobe (between the primary fissure and "the shallower fissura secunda"), and the posterior lobe (caudal to the secondary fissure). This concept is diagrammatically illustrated in figure 2. The criterion for the term primary fissure is clear, however, the criterion for the term secondary

fissure is not clear. A review of the literature on this matter has led this author to the conclusion that this term (secondary fissure) is a type of regressive phylogenetic designation. This means that the fissure was present in more complex cerebelli and its prescence was regressively traced (phylogenetically) to the very simple forms. Larsell (1952), in his monumental work on the cerebellum of the white rat, noted that a prominent fissure secunda was present in the 21 day fetus. Aciron in 1950 (Larsell, 1952) further noted that this fissure is distinct in the 35 mm rat embryo. Both of these authors also noted that other fissures were present in these early stages, therefore the possibility of embryological sequence would not necessarily hold, and consequently the term fissure secunda is open to criticism. Elliot Smith (1903a) also distinguished a band of cerebellar cortex that joined the paraflocculus to the pyramidal lobe of the vermis. On this problem he stated:

> "...it is desirable to have some term with which to distinguish the band of cortex linking the pyramid to the paraflocculus. I shall therefore call it the "copula pyramidis"."

The cerebelli of the tree shrews *Tupaia minor* and *Ptilocercus lowi* (pentailed tree shrew) have been briefly mentioned by Le Gros Clark (1924, 1926). In *Tupaia minor* the three main lobes and the two main fissures were noted (Fig. 2), a distinct copula pryamidis was present, and the anterior surface of the cerebellum was indented by the tectum of the mesencephalon. The copula pyramidis appeared to be "notched transversely" close to the paraflocculus, and no

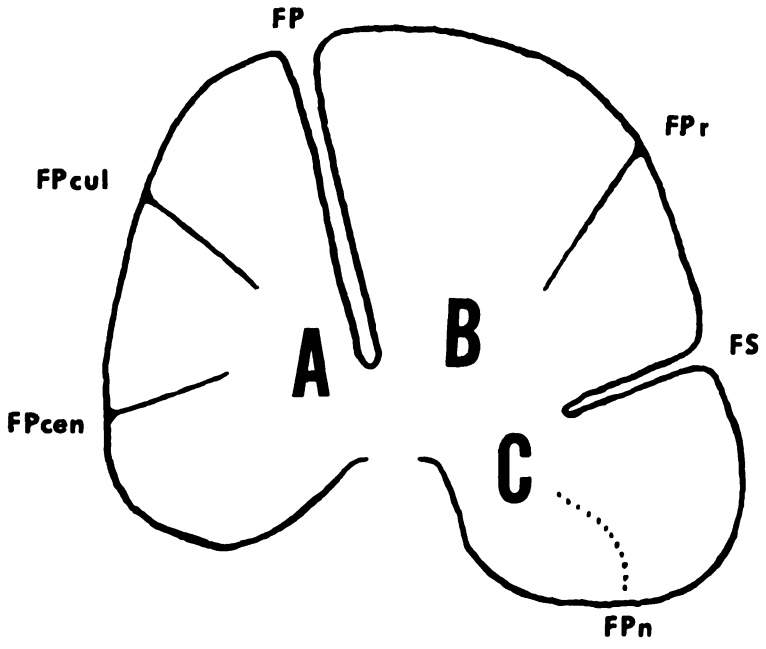


Fig. 2. Diagrammatic sagittal view of the general organization of the prosimian cerebellum as reported in the literature.

ABBREVIATIONS

A- anterior lobe	lingula central lobule culmen
B- middle lobe	median lobule pyramidal lobule
C- posterior lobe	uvula nodulus

FP - primary fissure
FPcen. - precentral fissure
FPcul. - preculminis fissure
FPn. - postnodular fissure
FPr. - prepyramidal fissure
FS - secondary fissure

distinct connection between the flocculus and nodulus was noted. (Consult table I for the review of flocculus and paraflocculus.) In *Ptilocercul lowi* (Le Gros Clark, 1926) the cerebellum is simpler in topography than *Tupaia*. The three main lobes and two main sulci are present. He further divided the anterior lobe into a lingula-central lobe region and a culmen by the fissure preculminis (Fig. 2). The middle lobe consists of the median lobule and pyramidal lobule, which is joined by a simple copula pyramidis. Behind the fissure secunda is the uvula and nodulus. In the *Tupaia* and *Ptilocercus* (Le Gros Clark 1924, 1926) the anterior and middle lobes have a varied number of short shallow sulci. The lateral hemispheres, which are principally lateral extensions of the median portion of the middle lobe, also have a varied number of sulci.

The cerebellum of *Tarsius* has been discussed by Elliot Smith (1903a), Woollard (1925) and Tilney (1927). Elliot Smith (1903a) noted that the topography of cerebellar cortex was more complex than either insectivora or marsupialia. The three main lobes are present and as noted by Tilney (1927), sulci rarely crossed from the vermis onto the lateral hemisphere. Woollard (1925) also noted three main lobes separated from each other by the fissure secunda and fissure prima. At this point it should be noted that the term fissure secunda begins to create confusion. Woollard (on *Tarsius*) states:

> "The fissura secunda or sulcus pre-pyramidalis lies on the sloping posterior surface of the cerebellum just in front of the pyramid."

This statement coupled with a careful study of the plates indicates that the secondary fissure of Elliot Smith (1903a) and the secondary fissure of Woollard (1925) are not the same. Woollard (1925), consequently, considers the pyramid as a component part of the posterior lobe. The relative position of the sulcus prepyramidalis of Woollard (1925) is indicated on figure 2. The medial and lateral portions of the middle lobe are creased by a variable number of sulci, and both the lingula and nodulus are hidden from view (Elliot Smith, 1903a; Woollard, 1925). The differing opinions on the relative size of the flocculus and paraflocculus are noted in table I (p. 84).

Kanagasuntheram and Mahran (1960) briefly discussed the cerebellum of the lesser galago *(Galago senegalensis senegalensis)*. They note a primary fissure, a secondary fissure, and the respective anterior middle and posterior lobes. The secondary fissure in this case is caudal to the pyramid of the vermis. The paraflocculus is associated with the pyramid of the vermis by the copula pyramidis which, according to these authors "...is hidden from the surface by the lateral portions of the middle lobe." A fissure preculminis is also noted (Fig. 2). Their fissure preculminis is caudal to the culmen and is termed fissure precentralis (Fig. 2) by other authors. The observations on the flocculus and paraflocculus are noted on Table I.

Krishnamurti (1966) reported on the cerebellum of the slow loris *(Nycticebus coucang coucang)*, and noted several basic differences. The greatly enlarged anterior lobe is divided into a culmen, central lobule and lingula by the fissures preculminis and precentralis

respectively. He also designated a prepyramidal fissure on the middle lobe and a secondary fissure separating middle and posterior lobes. Krishnamurti (1966) also noted that the copula pyramidis is almost completely hidden from view by the lateral extensions (hemispheres) of the middle lobe. The observations of the flocculus and paraflocculus are noted in table I.

It is appropriate at this point to clarify a conflict in the literature. The central lobe of Krishnamurti (1966) in the slow loris is between the culmen, which is directly rostral to the fissure prima, and the lingula. The central lobe of Kanagasuntheram and Mahran (1960) in the lesser galago is designated as that region directly rostral to the fissure prima. In other words, these authors have designated these two areas exactly opposite. This author, in view of this variability, has consulted the opinion of Crosby *et al.*, (1962) who also point out that the terminology applicable to the human cerebellum is not applicable to subhuman and subprimate forms. They further note that to the comparative neurologist the primary fissure is the primary landmark, and the main subdivisions of the anterior lobe are culmen, central lobule, and lingula in respective order from fissura prima to the anterior medullary velum. Since most investigators of the prosimian cerebellum refer to the culmen as the region directly rostral to the fissure prima, figure 2 has been drawn to conform to this general consensus.

Le Gros Clark (1931), in a study of the brain of the mouse lemer *(Microcebus murinus)*, noted that the cerebellum was simple and

resembled the same structure in *Tarsius*. A primary fissure and secondary fissure are present, and the corresponding 3 main lobes. The lateral lobes are small in relation to the vermis, and aside from the primary fissure only one shallow sulcus crossed from the vermis onto the hemisphere. The dispensation of the flocculus and paraflocculus can be noted in table I (p. 87).

The cerebelli of insectivores are very simple in structure and the terminology applied to prosimians is also applicable to this animal group. Elliot Smith (1902b) and Le Gros Clark (1928, 1932) have reported on the general anatomy of the cerebellum in a variety of insectivores and in the elephant shrew. In all cases a fissure prima and fissure secunda were present with the respective main lobes. The inconclusive observations on the flocculus and paraflocculus in this group are noted in table II. Le Gros Clark (1932) applied the term "post nodular fissure" to the deep groove between the uvula and the nodulus (dotted line - figure 2). This terminology has not been used in relation to any prosimian, only to insectivores.

The lateral hemispheres of the prosimian cerebellum are primarily lateral estensions of the middle lobe. Elliot Smith (1902a, 1903a, 1903b) designated three separate portions of the hemisphere as areas A, B, and C from rostral to caudal. The dopula pyramidis was occasionally referred to as area D. He described area A as the single folium caudal to the primary fissure; area B as the most lateral portion of the hemisphere and possessing a very narrow connection to the middle lobe; and area C as that portion between area B and the copula

pyramidis (area D). These regions and divisions are acknowledged for *Tupaia minor* and *Ptilocercus lowi* (Le Gros Clark, 1924; 1926) however no other investigator on the prosimian nervous system discussed these divisions. The available information on the hemispheres of the prosimian cerebellum is extremely vague.

Other reports of animals with a topographically simple cerebellum include those of Obenchain (1925) on small South American marsupials, Larsell (1952) and Zeman and Innes (1963) on the rat, and Dillon (1962) on monotremes. Pertinent studies on the cerebellum of the mouse include those of Miale and Sidman (1961), and Haddara and Nooreddin (1966).

CEREBELLAR CORTEX-CYTOARCHITECTURE

The cytoarchitecture of the cerebellar cortex has been investigated in a wide variety of mammalian and submammalian forms. Larsell and Jansen (1967) reviewed the literature on the vertebrates ranging from Hagfish to birds. The cytoarchitecture of the mammilian cerebellum has been studied by normal anatomical methods and by various degeneration techniques. Fox *et al.*, (1967) and Eccles *et al.*, (1967) have reviewed the pertinent literature, and the following brief description is from their works. The cerebellar cortex is made up of an outer molecular layer, a row of Purkinje cells, and an inner granular layer. The molecular layer is made up of two main cell types, the superior stellate cell and the inferior stellate cell, or more commonly called the basket cell. The superior (or outer) stellate cells come into synaptic relationship with the dendritic

field of the Purkinje cell, and the basket cell (inferior stellate) sends out a series of long processes that surround the cell body of the Purkinje cell. The Purkinje cell is the main efferent neuron of the cortex. Its dendritic field is compartmentalized upward into the molecular layer, and its single axon (with or without collaterals) descends from the underside of the cell body into the white matter. The granular layer contains the small (5-8 micra) granular cells with their characteristic claw-like terminations on the mossy fibers, and the larger (large stellate neurons) Golgi neurons. The granular cells in their terminations on the mossy fibers form the cerebellar or glomerular islands. The afferent fibers of the cortex are the mossy fibers and the climbing fibers. They have origin from the deep cerebellar nuclei as well as various brain stem regions (Eccles *et al.*, 1967) and are generally demonstrated by staining for degenerating fibers following specifically localized lesions.

A thorough review of the literature has revealed no available information on the cytoarchitecture of the cerebellar cortex for any prosimian primate. Due to certain consistent mammalian characheristics it is reasonable to assume that the prosimian cerebellar cortex will, in its general architecture, conform to that of the rhesus monkey (Fox *et al.*, 1967).

CEREBELLAR NUCLEI

It is well known that the cerebellum of man contains eight cerebellar nuclei, (Crosby *et al.*, 1962). In the anthropoid apes, and in the higher simian primates four morphological nuclei can be demon-

strated on each side (Ariens Kappers *et al.*, 1936; Cooper and Courville, 1968). It is equally well known that the cerebelli of dogs and cats contain three nuclei on each side (Flood & Jansen, 1961; Singer, 1962). In the lower Mammals (monotremes, marsupials, etc.) there are only two nuclei on each side, a roof nucleus and a lateral nucleus (Ariens Kappers *et al.*, 1936). No information could be found on the gross appearance or cytoarchitecture of the cerebellar nuclei in any prosimian primate. Obenchain (1925) in her study of small South American marsupials commented:

> "The deep nuclei form a pair of large oval masses almost meeting in the midline... there are only slight indications of differentiations into separate nuclei (dentate and roof nuclei)."

Tilney (1927) commented briefly on the cerebellar nuclei of *Tarsius*. He stated that they resemble the cerebellar nuclei of other low mammalian forms, and that they lack the size, definition and configuration of higher forms. However he does not have illustrations for his opinion, and he does not reference the "other low mammalian forms."

MATERIALS AND METHODS

GROSS EXAMINATION

The cerebelli of nine adult lesser bushbabies *(Galago senegalensis)*, and five adult tree shrews *(Tupaia glis)* were used in this study. The brains of two adult *Tupaia chinensis* also became available for this study. The *T. chinensis* were immersion-fixed (by the contributor) in formalin-Alcohol-Acetic acid without the skull being opened. Consequently, these two brains were used only in the gross portion of this study since they were inadequate for histologic study. The gross features of these two cerebelli were quite clear (folia, sulci, etc.) and subsequently contributed a great deal to the comparative value of this study. Some of the brains (in *G. senegalensis* and *T. glis*) were fixed by perfusion of the animals, while others were carefully removed and fixed by immersion in the appropriate fixative. The brain stem was transected at the level of the caudal mesencephalon and the cerebelli left attached to the pons and medulla to facilitate gross examination.

Gross examinations of the cortex were made bilaterally under a dissecting microscope using standard micro-dissecting instruments. Two dissecting scopes were used, a standard model, and one having a zoom lens. The latter allowed fine observation of the more discreet macroscopic points. In addition, drawings of the topography were made to the scale of 1 cm = 1 mm using calipers and a metric rule. All drawings were repeatedly checked for accuracy on horizontal, vertical and oblique angles.

FIXATION AND STAINING

A variety of histological techniques were used to illucidate the cytoarchitecture of the cortex and cerebellar nuclei. Cerebelli that had been perfusion-fixed and immersion-fixed were used for the histologic portion of this study. A variety of fixatives were used, depending on which stain or special technique was to be applied to a specific sample of tissue.

Fixation fluids for each stain or stain procedure used in this study.

Fix		Procedure
80% Alcohol		Thionin
10% BNF *		Einarson method
10% BNF *		Kluver and Barrera
15% BNF *		Cajal Method IV
100% Alcohol + 1-3 drop ammonia		Cajal Method III
chloral hydrate	-5-6gm	
100% Alcohol	-25cc	
HOH	-75cc	Cajal Method VI
5% potassium dichromate	-2pt	
1% Osmium tetroxide	-1pt	Rapid Golgi

* BNF = Buffered Neutral Formalin

The luxol fast blue-cresylecht violet method of Kluver and Barrera (1953) the gallocyanin method Einarson (1932), and a standard

thionin method (1959)[1] were used as Nissl stains. The luxol fast blue-cresylecht violet also served as a standard fiber-Nissl combination. Sections stained with the preceeding methods were cut at 8, 10, 12 and 20 micra on a rotary microtome.

Silver stains were employed to illucidate the cytological details of the cortex and cerebellar nuclei. The standard rapid-Golgi method (Conn *et al.*, 1962) was used, as were three methods of the Cajal reduced silver technique, Cajal Method III, IV, and VI (Jones, 1964). The specific fixative for each method is noted in table 3. The silver methods utilized in this study were block stains, and followed by dehydration and embedding in paraffin. The silver blocks were subsequently sectioned at 20, 25, 40, 50, 60, 70, 80 and 100 micra, mounted, coverslipped and stored in a dark place.

The drawings of the cerebellar nuclei were made with the aid of a Prado Universal projector[2] to insure accuracy. Every 10th or 20th section (indicated in each figure) was used and traced to show the progressive macroscopic appearance of the nuclei from rostral to caudal. The tracing of the nuclei was done on Luxol fast blue-cresylecht violet sections and confirmed on the gallocyanin stain.

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1. Clinical Laboratory Procedures: Pathological Anatomy Technique. U. S. Naval Medical School, Dept. of Navy. 1959.

2. Leitz Co., Germany.

RESULTS AND DISCUSSION

TOPOGRAPHY OF THE CEREBELLAR CORTEX

GENERAL INTRODUCTORY REMARKS

The criterion for dividing the cerebellum into main regions or lobes is not well established. Elliot Smith (1903a) suggested an anterior, middle and posterior lobe based on the recognition of a preclival (prima) fissure and a secondary fissure (fissura secunda). Bradley (1904, 1904-05) in an apparent effort to clarify the problem introduced the following method:

> "In order to avoid confusion, no pre-existing names were applied to these lobes and fissures, but the simplest method of designating them--that of letters and figures--was employed. The five lobes (...of the simplest workable type of cerebellum...) were called A, B, C, D, and E, commencing the enumeration with the most anterior, or rather with the one nearest to the anterior medullary velum. The fissures were similarly designated as I, II, III, and IV."

Comparing the methods of Elliot Smith (1903a) and Bradley (1904) one sees that the primary fissure and secondary fissure of Elliot Smith are fissure II and sub-fissure d respectively of Bradley. Anterior lobe A is area A & B, middle lobe B is area C, and posterior lobe C is area D & E, respectively, of each author. In the rat (Larsell, 1952) and avian (Larsell and Jansen, 1967) the method of numbering the folia from I-X has been utilized.

This designation resulted in the following classification:

I - lingula
II - ventral lobule centralis; sublobules a, b
III - dorsal lobule centralis; sublobules a, b
IV - ventral lobule culmenis
V - dorsal lobule culmenis
VI - declive; sublobules a, b, c, d
VII - tuber; sublobules a, b
VIII - pyramis
IX - uvula; sublobules a, b, c, d
X - nodulus

Crosby *et al.*, (1962) revert to a more basic and possibly more logic designation by suggesting only two main lobes; an anterior lobe rostral to the primary fissure, and a posterior lobe encompassing all portions caudal to the primary fissure.

The divisions of Elliot Smith (1903a), in one form or another. have been used by all investigators on the prosimian cerebellum. The methods of Bradley (1904, 1904-05) are rarely used and lead the reader into a great deal of confusion. The method used by Larsell (1952) for the rat has not been applied to the prosimian cerebelli; and since the primary fissure is the main landmark, the division of Crosby *et al.*, (1962) is certainly the most logical.

The primary fissure is the only consistently agreed upon landmark in all prosimian cerebelli, and all other simple mammalian cerebelli. It is deepest of all fissures, the only (or main) one to cross from the vermis into the hemisphere in the adult, and it appears early in the embryological development. Using this fissure as a landmark, it is suggested that all main fissures be named in order rostrally and caudally from this point. Rostrally there is a precentral fissure and a postcentral fissure (prelingual), and

caudally a prepyramidal fissure, postpyramidal fissure, and a prenodular fissure. This terminology employs the only agreeable landmark, designates the fissures in order rostrally and caudally in relationship to the main regions of the vermis, and is entirely applicable to both *Galago* and *Tupaia* (Fig. 3 and 6). It is further suggested that this designation of main fissures be used in all prosimian cerebelli because of a general lack of a basic criterion for naming fissures in the adult animal. The above mentioned terms will be used throughout the remainder of this study.

The method used by Larsell (1952) for the rat for designating the vermal folia I-X is partially applicable to the prosimian cerebellum and modifications of his method will be used. It is extremely confusing to designate gyri and sulci by only upper or lower case letters or numbers (illustrated by reading Bradley), therefore all folia or groups of folia will be named. The best and most applicable term presently applied to any specific region will be retained, and for those areas not presently named, a justifiable term will be drawn from the comparative literature.

GALAGO SENEGALENSIS

The lesser bushbabies used in this study are adult, therefore all discussion is of the adult form. No attempt is made to suggest embryological origin of any part, since this would be pure conjecture.

The lesser bushbaby *(Galago senegalensis)* is found throughout most of Africa south of the Sahara (Hill, 1953). The most striking behavioural characteristic of the *Galago* is its mode of locomotion.

They move by leaping on their hind limbs, the leap being as much as 10 feet in an oblique direction (Hill, 1953) or 7 feet, 4.75 inches in a vertical direction (Hall-Craggs, 1965). This mode of progression requires this animal to have a keen sense of forward and backward balance. When not in a stress situation the *Galago* will proceed in a quadrapedal manner (personal observations), however the usual mode of locomotion is via a hopping attitude. They also demonstrate a good sense of balance by assuming an entirely erect posture, from a squatting position, with great rapidity.

Mid-Sagittal Section

A mid-sagittal view of the *Galago* cerebellum (Fig. 3) illustrates a structure of moderate complexity. The primary fissure is the deepest fissure, and has within its bounds three main folia on its rostral and caudal aspects. The sulci within the primary fissure are continuous from the vermis into that portion of the fissure that extends into the lateral hemisphere. This is the case only for the primary fissure, the sulci in all other main fissures are restricted to the vermal portion of their respective lobes and have no continuation into the hemisphere. The primary fissure divides the cerebellum, on mid-sagittal view, into two main lobes of almost equal size. The anterior lobe rostral to, and the posterior lobe caudal to the primary fissure. The nodulus of the posterior lobe is technically part of the flocculonodular complex.

Anterior lobe

The anterior lobe is divided by a precentral fissure and a postcentral fissure (prelingual fissure) into a culmen lobule, central lobule and lingual lobule respectively (Fig. 3, 5). When the cerebellum is viewed from its lateral aspect (Fig. 4) it is noted that the primary fissure is continuous into the hemisphere, consequently the culmen has a hemispheric portion. It is further noted that the precentral fissure is also continuous into the hemisphere subsequently giving rise to a hemispheric portion of the central lobule (Fig. 5).

The hemispheric portions of the culmen lobule and central lobule, to this investigator's knowledge have not been described, or had any adequate term applied to them. In the *Galago* the culmen passes into the hemisphere and decreases in size until becoming attenuated into a single folium directly adjacent (medially) to the flocculus (Fig. 4). The hemispheric portion of the culmen is roughly pyramidal in shape, the base of the pyramid located at the hemisphere-vermis junction (Fig. 6). The hemispheric extension of the central lobe also comes into close apposition to the flocculus, but it does not taper as it passes laterally (Fig. 5). The vermal portions of the culmen and central lobules are designated as vermal culmen and vermal central lobule respectively (Fig. 4, 5). The hemispheric portions of each lobule are designated as culmen pars lateralis and central lobule pars lateralis respectively (Fig. 4, 5). Specific terminology is justified for these regions because it

appears that lateral extensions of the vermal culmen and vermal central lobule tend to be primate characteristics since this condition is not seen in some advanced subprimate mammalian forms (Larsell, 1953) excepting the monotremes (Dillon, 1962).

The culmen, central lobule and lingula have a characteristic number of intrinsic sulci. An intrinsic sulcus is defined as one which does not communicate with the edge of a folium or lobule, or with another fissure or sulcus. In the culmen there are always three (Fig. 5) and occasionally four intrinsic sulci (Fig. 3) dividing the culmen into 4-5 folia. The most superior sulcus (Fig. 3) is shallow, confined to the vermis, and the one that is usually not present. This sulcus is not illustrated in Figure 5. These sulci extend into the culmen pars lateralis but end before reaching its lateral boundary. The central lobule has two intrinsic sulci, one limited to the vermal central lobule and one continuous into the central lobule pars lateralis (Fig. 5). The lingula has a single intrinsic folium, which is rarely absent (Fig. 3). The fissure between the lingula and central lobule does not continue into the hemisphere, is relatively deep, and distinctly separates the vermal central lobule and the lingula (Fig. 3, 5). Therefore the terms post central fissure and prelingual fissure and considered synonymous.

The numerical method of Larsell (1952, 1953) can be applied to the *Galago* with minor modifications. The lingula is composed of sublobules Ia and Ib; the first folium of the vermal central lobule

is lobule II and the upper two folia are indicated as sublobules IIIa and IIIb (Fig. 3, 5). This division of the central lobule is based on the fact that the first intrinsic sulcus is not only the deepest, but is also continuous into the central lobule pars lateralis (Fig. 5). The vermal culmen is composed, in most cases, of four main folia. Just above the precentral fissure are sublobules IVa and IVb, and just rostral to the primary fissure are sublobules Va and Vb (Fig. 3). Sublobule Vb is on rare occasion divided by a very shallow superficial fissure. The same criterion used on the central lobe is applied to the culmen. Those folia separated by sulci that are continuous into the culmen pars lateralis are designated as lobule IV (sublobule a & b), and folia separated by sulci limited to the vermal culmen as lobule V (sublobule a & b) (Fig. 5).

Posterior Lobe

A sagittal section of the cerebellum reveals the four main lobules of the posterior half of the *Galago* cerebellum; the median lobule (of Elliot Smith 1903a), the pyramidal lobule, the uvular lobule and the nodular lobule. The pyramidal lobule of the vermis and the nodular portion of the flocculonodular lobule (Crosby *et al.*, 1962) must be considered at this time even though these areas will be discussed again later (cf Flocculus and Parafloccullus).

The first main division of the posterior lobe is composed of the declive and the tuber (Fig. 4, 5). Elliot Smith (1903a) divided the prosimian hemisphere into three areas, merely designating them

as areas A, B, and C from rostral to caudal. His area A was the single folium just caudal to the fissure prima, which he later designated as the area lunata (1903b). A more widely used and more acceptable term for this area is lobulus simplex (Fig. 4) (Crosby *et al.*, 1962). In the *Galago* simplex is represented on sagittal view by the uppermost folium on the caudal wall of the primary fissure. In about half of the *Galagos* examined the lobulus simplex was divided by an intrinsic sulcus into two narrow folia. When this occurs there is a superficial representation of the simplex in the vermis just rostral to the remainder of the declive (Fig. 4). In animals with a single large lobulus simplex there is no superficially visible portion in the vermis. The fissure separating the lobulus simplex from the rest of the hemisphere crosses the midline (Fig. 3) and continues to the lateral extent of the hemisphere (Fig. 4). As this fissure passes from the vermis into the hemisphere it essentially rises out of the fissure prima to become visible on the surface, in doing so it courses slightly caudal, then passes laterally to the margin of the hemisphere (Fig. 4, 5). The term posterior superior fissure has been applied to this fissure in the rat, cat and monkey (Larsell 1952, 1953) and it is the post clival fissure in man (Crosby *et al.*, 1962). Since there is no anterior superior fissure in these adult animals, the former terminology is confusing. It is therefore suggested, in an effort to have adequate yet accurate terminology, that the term simplex fissure be applied to this fissure in the prosimian cerebellum (Fig. 3, 4, 5). The main superficially visible region of

the vermis caudal to the fissure prima is the remaining portion of the declive (Fig. 3). These two folia have no direct continuation into the hemisphere. Lateral to the declive and separated from the caudal area of the hemisphere by a second deep fissure is the ansiform lobule (Fig. 4). (It should be noted at this point that the reference to portions of the hemisphere that are "lateral" to portions of the vermis (i.e. declive) is based on the anatomical juxta-position of fissures and folia. This medial-lateral association of one part of the vermis to one part of the hemisphere is not intended to indicate a functional association but only a gross anatomical relationship based on the continuation of folia, and/or fissures from the vermis onto the hemisphere, or the close apposition of main folia and fissure in these areas. This criterion should be kept in mind during the remainder of all topographical discussion.) In the *Galago* this lobule is made up of two folia separated by a deep intercrural fissure, the rostral folia is interpreted as crus I and the caudal folia as crus II of the ansiform lobule (Fig. 5). A slight variation of the large single folium making up crus I is noted in the same animals that have a sulcus in the lobus simplex (page 28). In the specimens with a sulcus in the lobulus simplex a very shallow and superficial sulcus is also present in crus I of the ansiform lobule (Fig. 4). This is an intrinsic sulcus, and even when it is present the overall size of crus I does not change. Caudal to the declive of the vermis is the single folium of the tuber, also designated as lobule VII. The tuber is occasionally visible on the surface (Fig. 3) but usually it

is overlapped by the declive which forces it down into the prepyramidal fissure at the sagittal level (Fig. 4, 5). The remaining portion of the hemisphere which is lateral to the tuber and caudal to the ansiform lobule is the paramedian lobule. It is consistently made up of four folia, the last of which is hidden from view within the fissure between the copula and the paramedian lobule (Fig. 5). The deep fissure separating the ansiform and paramedian lobules in the *Galago* begins in the midline (Fig. 3), passes laterally and caudally at the vermal-hemisphere junction (Fig. 5, 6), and then continues laterally to the margin of the hemisphere (Fig. 5). The term ansoparamedian fissure has been applied to this fissure in the rat (Larsell, 1952), and this term is appropriately applied to this fissure in the *Galago* (Fig. 4, 5).

Elliot Smith (1903a) defined that broad band of cortex connecting the paraflocculus to the pyramidal lobule as the copula pyramidis. In the lesser bushbaby what appears to be the lowest folia of the hemisphere is actually the copula pyramidis (Fig. 4). It is slightly foliated by being subdivided by one or two intrinsic longitudinal sulci. The copula will be described in more detail later (cf Flocculus and Paraflocculus).

The prepyramidal fissure separates the tuber of the vermis from the pyramidal lobule (Fig. 3, 4). It is moderately deep and has two or three folia within its bounds. Larsell (1952) has shown that in the early embryonic stages of the rat the cerebellum is essentially a bulbus plate crossed by the developing fissures. The prepyramidal fissure appears early and eventually runs from the midline of the

developing hemisphere. It separates those embryonic areas which will eventually differentiate into the paramedian lobule and the copula pyramidis. As the paramedian lobule grows it pushes the lateral part of the prepyramidal fissure caudal. The fissure therefore essentially extends from the midline to the hemisphere-vermis junction, continues caudally for a short distance as part of the deep paramedian sulcus (discussed later), then extends laterally to separate the lowest visible paramedian folium from the copula (Fig. 4, 5). The term prepyramidal fissure is suggested for and applied to the entire extent of this fissure even to its lateral termination.

The pyramidal lobule in *Galago* is consistently divided into three folia designated as sublobules VIIIa, VIIIb and VIIIc (Fig. 3). These folia are intrinsic to the vermis and, excepting its connection to the copula (discussed later) the pyramidal lobe has no lateral representation in the hemisphere. The sulci of this lobe are also intrinsic and have no lateral counterparts in the hemisphere.

On the sloping caudal surface of the *Galago* cerebellum the hemisphere is sharply separated from the vermis (Fig. 4) by a deep groove, the paramedian sulcus. As previously mentioned the prepyramidal fissure assists in the formation of this groove as it courses caudally and laterally (Fig. 13). There is no indication of a paramedian sulcus on the anterior surface of the cerebellum since about half of the anterior lobe (II, IIIa & b, IVa & b) is directly in contact with the caudal colliculus of the mesencephalon.

The postpyramidal fissure separates the pyramid from the uvula

(Fig. 3, 4). In the white rat embryo the postpyramidal fissure (Fissura secunda of Larsell) extends laterally separating the early paraflocculus into dorsal and ventral parts (Larsell, 1952). In the adult *Galago* no lateral extension of the postpyramidal fissure is seen. In both macroscopic observations and in tracing this fissure from medial to lateral in microscopic serial sections it appears to stop at the vermis hemisphere junction. Two possible explanations of this are offered later (cf Flocculus and Paraflocculus). It is possible that the lateral portions of the postpyramidal fissure are represented by the groove between the copula pyramidis and the flocculonodular bundle.

The uvula has three folia designated as sublobule IXa, IXb and IXc, which do not have hemispheric representation in the adult *Galago*.

The nodulus is separated from the uvula by the prevodular fissure, one of the deepest fissures in the adult cerebellum (Fig. 3, 5). The term posterolateral fissure has been applied to that fissure separating the uvula-ventral paraflocculus portion of the developing cerebellum from the nodulus-flocculus portion (Larsell, 1952). In the adult *Galago* this fissure does not appear to continue into the hemisphere, but rather it ends just lateral to the nodulus. The details of the flocculonodular relationships are discussed under the heading Flocculus and Paraflocculus.

The most caudal lobule of the cerebellar vermis is the nodulus (Fig. 3). It invaginates the posterior medullary velum and helps to form part of the caudal wall of the fourth ventricle. The nodulus

is designated as lobule X with no sublobules being indicated since these subdivisions were not entirely consistent. There were usually two subdivisions, a large caudal sublobule and a larger rostral sublobule, sometimes three sublobules were seen and rarely four. In view of the inconsistent pattern, the only designation of the nodulus will be lobule X.

ABBREVIATIONS FOR FIGURES 3, 4 and 5

ANS - ansiform lobe
CVL - vermal central lobule
CLPL - central lobule pars lateralis
CP - copula pyramidis
CPL - culmen pars lateralis
Cr.I - crus I of ansiform lobule
Cr.II - crus II of ansiform lobule
CV - vermal culmen
D - declive
FAP - ansoparamedian fissure
FP - fissura prima
FPccn. - precentral fissure
FPn. - prenodular fissure
FPo. - postpyramidal fissure
FPoC. - postcentral fissure
FPr. - prepyramidal fissure
FS - simplex fissure
L - lingula
LS - lobus simplex
N - nodulus
P - position of the paraflocculer stalk
PM - paramedian lobule
PMS - paramedian sulcus
PY - pyramidal lobule
T - tuber
U - uvula

I - lingula: sublobules Ia, Ib
II - ventral central lobule
III - dorsal central lobule: sublobules IIIa, IIIb
IV - ventral culmen: sublobules IVa, IVb
V - dorsal culmen: sublobules Va, Vb
VI - declive: sublobules VIa, VIb
VII - tuber
VIII - pyramidal lobule: sublobules VIIIa, VIIIb, VIIIc
IX - uvula: sublobules IXa, IXb, IXc
X - nodulus

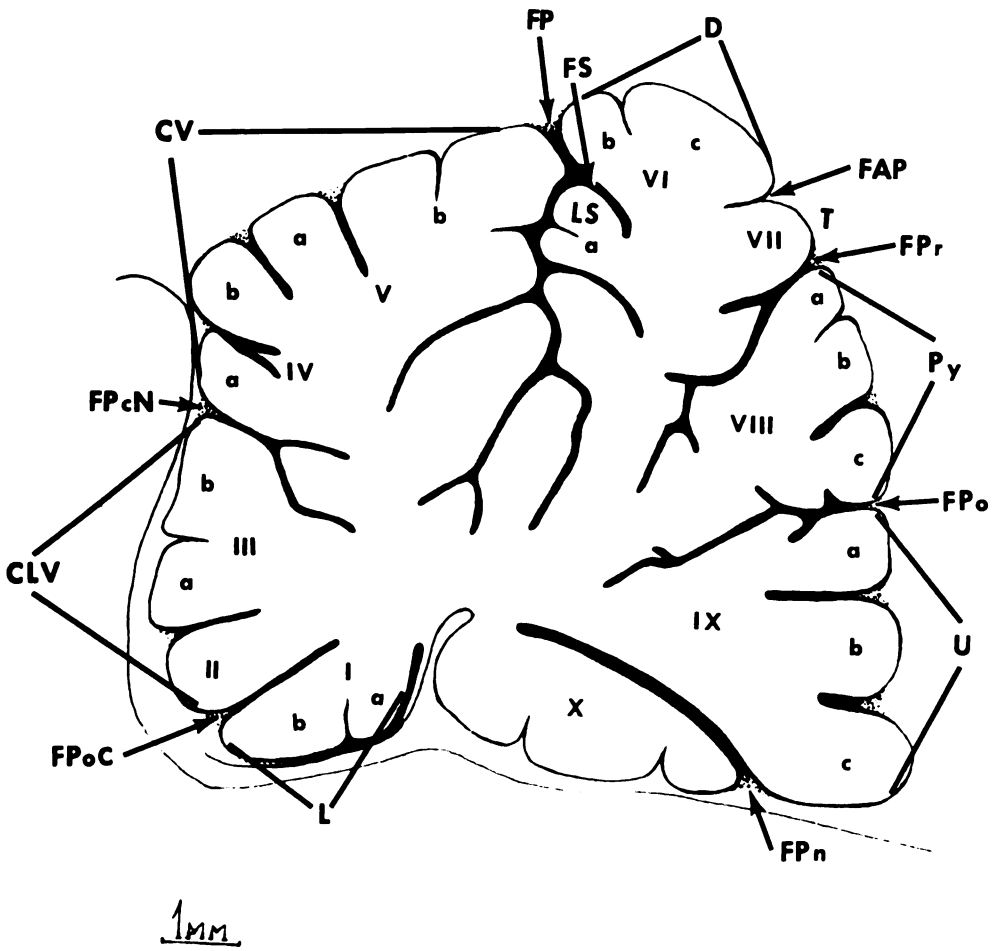


Figure 3. Mid-sagittal view of the cerebellum of the lesser bushbaby *(Galago)*.

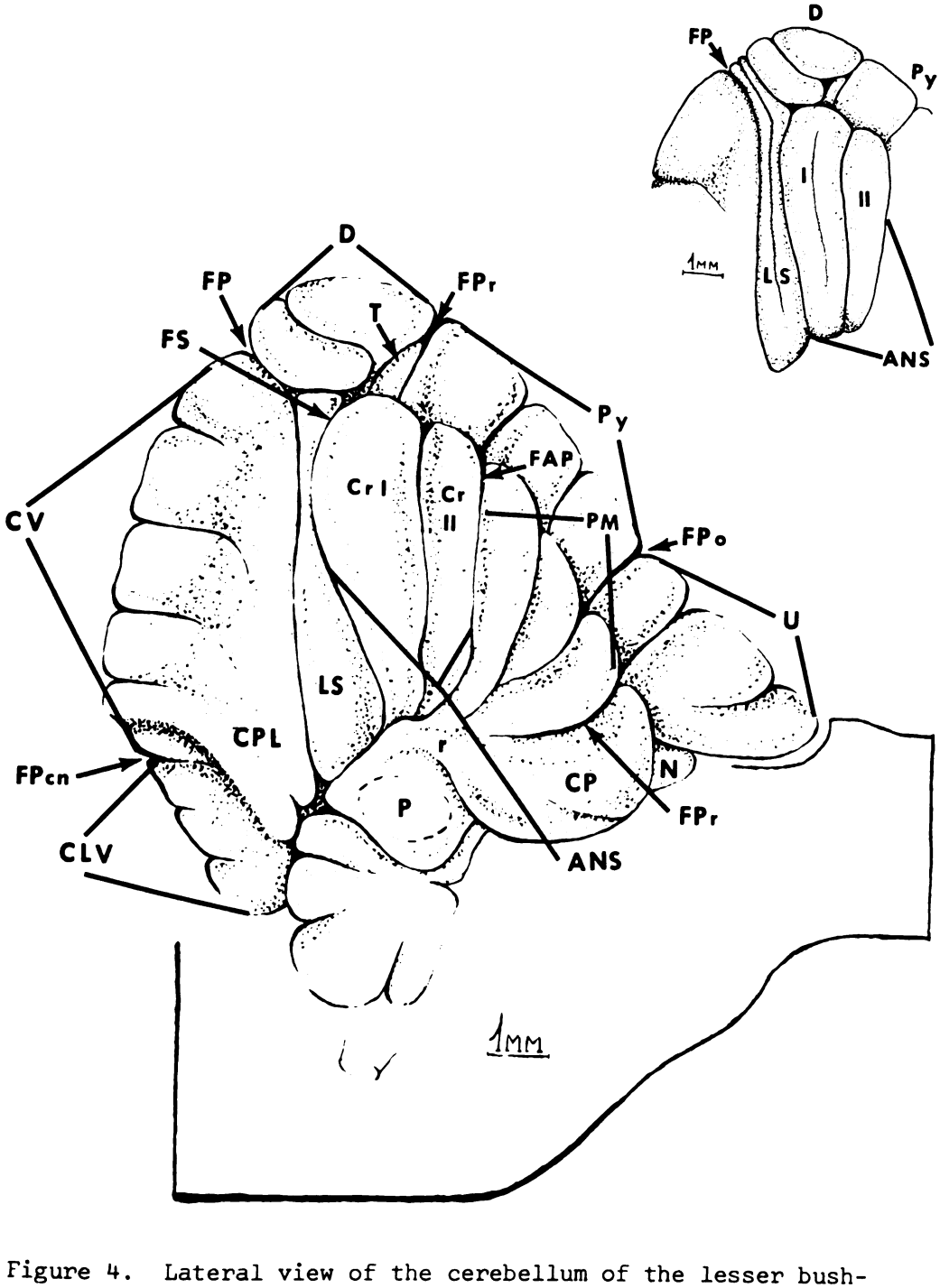


Figure 4. Lateral view of the cerebellum of the lesser bush-baby *(Galago)*. The paraflocculus has been removed (P) for sake of clarity. The inset illustrates the variation seen in the lobus simplex (LS) and crus I of the ansiform lobule. It is noted that when the lobulus simplex is fissured it is also superficially visible in the vermis.

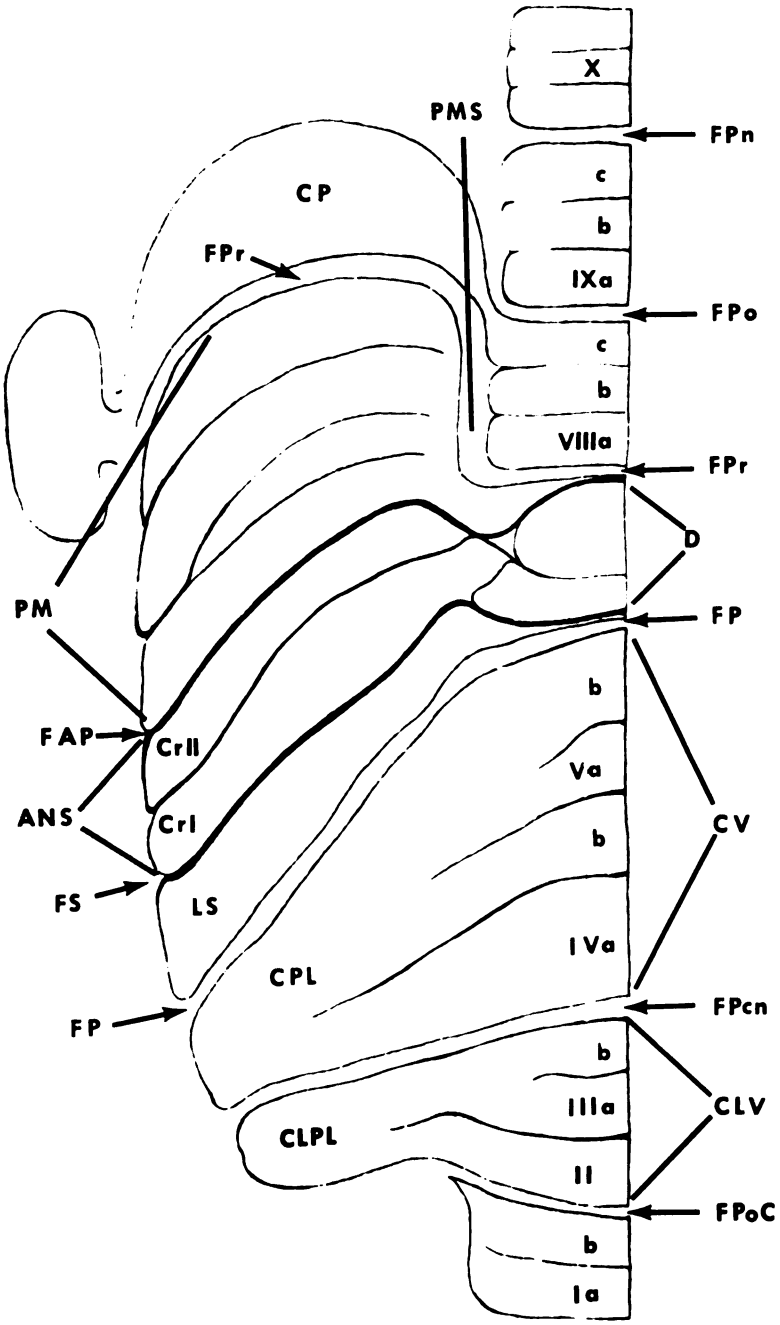


Figure 5. A semi-diagrammatic drawing of the cerebellar cortex in the lesser bushbaby *(Galago)*. This drawing represents only those portions of the cortex that are superficially visible, and it is longitudinally flattened so the entire cortex is illustrated on one plane.

TUPAIA GLIS AND *TUPAIA CHINENSIS*

The tree shrews used in this study are adult; therefore all morphologic points of discussion, both gross and microscopic are for the adult forms. Any attempt to suggest the embryological development of a particular part is pure conjecture. The discussion of the gross anatomy of the *Tupaia* cerebellum includes *T. glis* and *T. chinensis*, since it is usually applicable to both species. When specific and consistent differences are noted between these animals they are discussed separately and a conclusion is drawn concerning a particular point of difference. In the overall plan the cerebelli of these two species of *Tupaia* are strikingly similar, and only a few differences are noted.

The tree shrew *(T. glis* and *T. chinensis)* is found in India, throughout South East Asia, Thailand and on many of the off-shore islands in this region (Napier and Napier, 1967). The tree shrew is about 1/4 smaller than the *Galago*, quadrupedal, and moves about with "jerky scurrying movements" such as a rodent. *Tupaia* may jump from branch to branch over short distances but is believed to move about mainly on the forest floor (Napier and Napier, 1967). In the tree shrew, because of its mode of locomotion, there is less need for balance and fine digital sense, a point of particular significance.

Mid-sagittal section

A mid-sagittal view of the *Tupaia* cerebellum reveals a moderately complex structure compared to the *Galago* and rat (Larsell, 1952) (Fig. 6). A distinct deep primary fissure is present and it appears

to divide the cerebellum into almost equal anterior and posterior lobes. However this fissure does not pass into the hemisphere but extends rostrally over the anterior surface of the hemisphere ending at what essentially is the junction of the hemisphere and vermis (Fig. 8, 9). Consequently the sulci within the fissure prima are restricted to the vermis.

Anterior Lobe

The anterior lobe of the tree shrew cerebellum is divided into a culmen, central lobule and lingula by the precentral and postcentral fissures respectively (Fig. 6, 7, 9). The criterion for this method of naming fissures is discussed on page 23. Considering the position of the primary fissure it is therefore noted that the anterior lobe is restricted to the vermis (Fig. 8, 9).

The lingula invaginates the anterior medullary velum and is distinctly separated from the central lobule by a deep prelingual (postcentral) fissure (Fig. 6). The lingula has no intrinsic sulci and no continuations into the hemisphere (Fig. 8). The method of Larsell (1952) is applicable to the tree shrew when slightly modified, thus the lingula is indicated as lobule I (Fig. 6).

The central lobule is completely separated from the culmen and lingula by the precentral and postcentral fissures respectively (Fig. 6, 9). A characteristic number of intrinsic and extrinsic fissures are noted for the central lobule. The term, intrinsic sulci, has been defined, and an extrinsic sulci is defined as one which reaches the edge of a main lobe (or lobule) thus dividing the

lobe (or lobule) in a more definite and distinct manner. The central lobule has a single extrinsic sulcus dividing it into a large upper portion and a slightly smaller lower portion (FIC-Fig. 7). The upper and lower portions of the central lobule are each divided by a single intrinsic sulcus (Fig. 8, 9). The intrinsic sulcus of the upper portion will sometimes reach the margin, however when it does it is very shallow at this point, and even this very shallow continuation is sometimes absent. The entire central lobule of *Tupaia* is vermal (i.e. vermal central lobule) and there is no hemispheric representation (i.e. central lobule pars lateralis). The lower portion of the vermal central lobule consists of two folia designated as sublobules IIa and IIb (Fig. 6). The upper portion of the vermal central lobule, even though collectively it is larger, also consists of two folia designated as sublobules IIIa and IIIb (Fig. 6). The intercentral fissure is the division between the upper and lower portions of the vermal central lobule because it is not only the deepest fissure but it is also the only fissure to consistently reach the lateral margin of the central lobule.

The culmen (vermal culmen) is separated from the posterior half of the cerebellum by the deep primary fissure and from the central lobule by the moderately deep precentral fissure (Fig. 6, 8, 9). The vermal culmen of *Tupaia* is also characterized by a single distinct extrinsic fissure dividing it into about equal halves. This interculmen fissure reaches the lateral extent of the culmen dividing it into an upper and lower portion (Fig. 9). These two regions end

before becoming part of the hemisphere. The ventral portion ends before reaching the margin, while the dorsal portion extends laterally then anteriorly to the margin of the cerebellar cortex (Fig. 9). In one brain of *Tupaia chinensis* both portions of the culmen extended (anteriorly) to the margin of the cerebellum, so a small degree of variation can be expected to occur at this point. The upper and lower portions of the vermal culmen are each divided by a single intrinsic sulcus. These sulci travel only a short distance from the midline, then disappear (Fig. 7c8). They are consistent and indicated as sublobules IVa and IVb for the lower portion and sublobules Va and Vb for the upper portion of the vermal culmen (Fig. 6).

The primary fissure separates what has been shown to be a rather modest anterior lobe from the expanded hemisphere. The anterior lobe is considered to be modest in its development because it essentially has no more than the vermal components of all its lobules, with no representation in the hemisphere.

Posterior Lobe

The posterior lobe of the cerebellum of the tree shrew (excepting the technicality of a flocculonodular lobule) is composed of a median lobule (declive-tuber), a pyramidal lobule, a uvular lobule and a nodular lobule (Fig. 6,7,8). Since there is no culmen pars lateralis and central lobule pars lateralis, the primary fissure extends from the midline laterally then rostrally (essentially over the front of the hemisphere) separating the hemisphere from the vermal culmen

(Fig. 7,8,9). The primary fissure is deep on the sagittal plan but rapidly diminishes in depth as it progresses laterally. Directly caudal to the fissura prima on the vermis are the flat folia comprising the lobus simplex of the declive (Fig. 7,8). In the *Tupaia glis* the lobus simplex portion of the declive is composed of two folia. The sulcus separating these two folia is shallow and is not continuous with its counterpart from the hemisphere (Fig. 7). In *T. glis* these two medial folia of the lobulus simplex fade into a single large lateral lobulus simplex which extends laterally and rostrally onto the anterior surface of the hemisphere (Fig. 8,9). In *Tupaia chinensis* the lobulus simplex of the declive is a single broad folium that is as wide as the lobulus simplex of *T. glis*, however it is not divided by the shallow intrinsic sulcus (Fig. 6). The simplex sulcus (Fig. 8c9) begins at the hemisphere-vermis junction and extends from the dorsal surface of the hemisphere (Fig. 8) onto its anterior surface (Fig. 9). The term lobulus simplex is applicable to both the vermal and hemispheric portions of this region. Based on the comparison of the lobus simplex of *T. glis* with *T. chinensis*, this region is designated as lobule VIa in *Tupaia chinensis* and in *Tupaia glis*. The reason for this will soon be apparent.

Caudal to the superficially visible lobulus simplex is the remainder of the declive region of the vermis. It is made up of one slightly larger folia, and two slightly smaller ones (Fig. 7,8). These are designated as sublobules VIb, IVc and IVd (Fig. 6,8). Sublobule VIb is occasionally subdivided by a very shallow sulcus,

however this does not appear to be a significant occurrence, and none of the sulci of the declive are directly continuous into any corresponding fissure or sulcus in the hemisphere (Fig. 8).

The single folium caudal to the declive of the vermis and slightly enlarged in its lateral extent is the tuber (Fig. 7, 8). It is undivided and is usually separated from the hemisphere by a consistent shallow sulcus (Fig. 8). The tuber is separated from the pyramidal lobule by the deep prepyramidal fissure and being consistently single is designated as lobule VII.

The reasons for suggesting the two folia of the lobus simplex of *T. glis* as sublobule VIa are now apparent. In both *T. glis* and *T. chinensis* the declive is composed of three folia and the tuber of one. Even though the lobulus simplex of *T. chinensis* is not subdivided as it is in *T. glis* it is just as large. Secondly the subdivision in *T. glis*, when viewed by itself, does not appear to be a significant sulcus. It is therefore concluded that this division of the vermal portion of the lobus simplex in *T. glis* is only a slight modification of a distinct general plan and not worthy of the classification of sublobules.

Even though none of the sulci of the vermis are directly continuous with those of the hemisphere, there are two main fissures which come into close apposition with the vermis (Fig. 8). The first is the simplex fissure, the second is the ansoparamedian fissure (Fig. 7, 8). By nature of their configuration and apposition to the fissures and sulci of the vermis, it appears that the declive of the

vermis is adjacent laterally partially with the ansiform lobe and partially with the paramedian lobe (Fig. 7, 8).

The ansiform lobule of the *Tupaia* is made up of five folia (Fig. 7, 8). This lobule is distinctly separated from the rest of the hemisphere by the simplex fissure and ansoparamedian fissure. Within this large ansiform area, a fissure of secondary importance is noted. It is deep, approaches more closely to the vermis than any other fissure within the lobe, and consistently divides the rostral three ansiform folia from the caudal two folia (Fig. 7, 8). For clarity sake this cleft will be termed the intercrural sulcus (after Larsell, 1952, 1953). The intercrural sulcus divides the rostral three folia, interpreted as crus I, from the caudal two folia interpreted as crus II (Fig. 7). In both of the *Tupaia* in this study crus I is consistently composed of three folia, of which the middle one is the largest. Crus II in *Tupaia glis* is made up of two folia separated by a shallow sulcus (Fig. 7) while in *Tupaia chinensis* the sulcus is absent but the resulting single folium is wide. Crus I and crus II of the ansiform lobe make up the majority of the anterior and lateral surface of the hemisphere indicating a state of relatively advanced development for this particular region.

The large portion of the hemisphere lateral to the tuber and caudal to the ansoparamedian fissure is the paramedian lobule (Fig. 7, 8). The paramedian lobule is made up of four caudally buldging folia making up the caudal surface of the hemisphere, and separated from the vermis by a deep groove, the paramedian fissure (Fig. 7, 8). The uppermost

folium of the paramedian lobule extends above the level of the ansiform lobes crus I and crus II (Fig. 9). There is no indication of a paramedian groove, sulcus, or fissure on the dorsal or anterior aspects of the *Tupaia* cerebellum (Fig. 7,9).

The prepyramidal fissure separates the tuber from the pyramidal lobule of the vermis. This fissure is moderately deep on the midline, extends laterally then caudally (as part of the paramedian fissure) then again courses laterally around the hemisphere separating the paramedian lobule from the copula pyramidis (Fig. 7,8). It is suggested that the term prepyramidal fissure be used for this fissure from the midline to its lateral extent. The pyramidal lobule in *T. glis* and *T. chinensis* is consistently composed of two folia of about equal size. These are designated as sublobules VIIIa and VIIIb of the pyramidal lobule.

What appears to be the lower most folium of the hemisphere is part of the copula pyramidis (Fig. 7). In the tree shrew the copula is differentiated into a copula pyramidis lateralis and a copula pyramidis medilis (Fig. 7). The copula pyramidis lateralis is a small tear-drop shaped folium very closely associated with the paraflocculus and overhung by certain regions of the ansiform lobule. The copula pyramidis medialis is the narrow band of cerebellar cortex that is continuous with the pyramidal lobule of the vermis. The details of these relationships will be discussed later (cf Flocculus and Paraflocculus).

The postpyramidal fissure separates the pyramidal lobule and

the uvular lobule, and in the adult animal has no macroscopically lateral continuation. The uvula of *Tupaia glis* is usually composed of what appears to be four main folia (Fig. 6). The uvula of *Tupaia chinensis* is made up of only two main folia and appears, with the exception of the extra folia, to closely resemble the same structure in *T. glis*. (Fig. 6). Based on this comparison within *Tupaia* this sulcus is termed the interuvular sulcus, the sublobules are designated IXa and IXb (Fig. 6). It should again be noted and emphasized that the variation between the uvula of *T. glis* and that of *T. chinensis* is relatively minor while the general concept of two sublobules is quite acceptable. The two extra intrinsic sulci in the uvula of *T. glis* are not deep significant sulci therefore the added sublobules created by these are not considered significant enough to merit a separate classification.

The prenodular fissure also appears to have no lateral continuation yet affords a distinct separation between the uvula and nodular lobules. The nodulus of the tree shrew appears to have a fairly consistent pattern. In *T. glis* two large ventral folia and an occasional small dorsal folium is noted. The *T. chinensis* has only the two ventral folia. In view of this consistency of a general pattern these folia are designated as sublobules Xa and Xb. The sulci of the uvula and nodulus are intrinsic and these lobules have no representation in the hemisphere. The flocculo-nodular relationships are discussed later (cf Flocculus and Paraflocculus).

ABBREVIATIONS FOR FIGURES 6, 7, 8, and 9

ANS - ansiform lobule
CLV - vermal central lobule
CP - copula pyramidis
CPL - copula pyramidis lateralis
CPM - copula pyramidis medialis
Cr. I - crus I of ansiform lobule
Cr. II - crus II of ansiform lobule
CV - vermal culmen
D - declive
FAP - ansoparamedian fissure
FIC - intercentral fissure
FICL - interculmen fissure
FP - primary fissure
FPcn. - precentral fissure
FPn. - prenodular fissure
FPo. - postpyramidal fissure
FPoC. - postcentral fissure
FPr. - prepyramidal fissure
FS - simplex fissure
ICS - intercrural sulcus
IUS - interuvular sulcus
L - lingula
LS - lobus simplex
N - nodulus
P - position of the paraflocculer stalk
PM - paramedian lobule
PMS - paramedian sulcus
T - tuber
U - uvula

I - lingula
II - ventral central lobule: sublobules IIa, IIb
III - dorsal central lobule: sublobules IIIa, IIIb
IV - ventral culmen: sublobules IVa, IVb
V - dorsal culmen: sublobules Va, Vb
VI - lobulus simplex and declive: sublobules VIa, VIb, VIc, VId
VII - tuber
VIII - pyramidal lobule: sublobules VIIIa, VIIIb
IX - uvula: sublobules IXa, IAb
X - nodulus: sublobules Xa, Xb

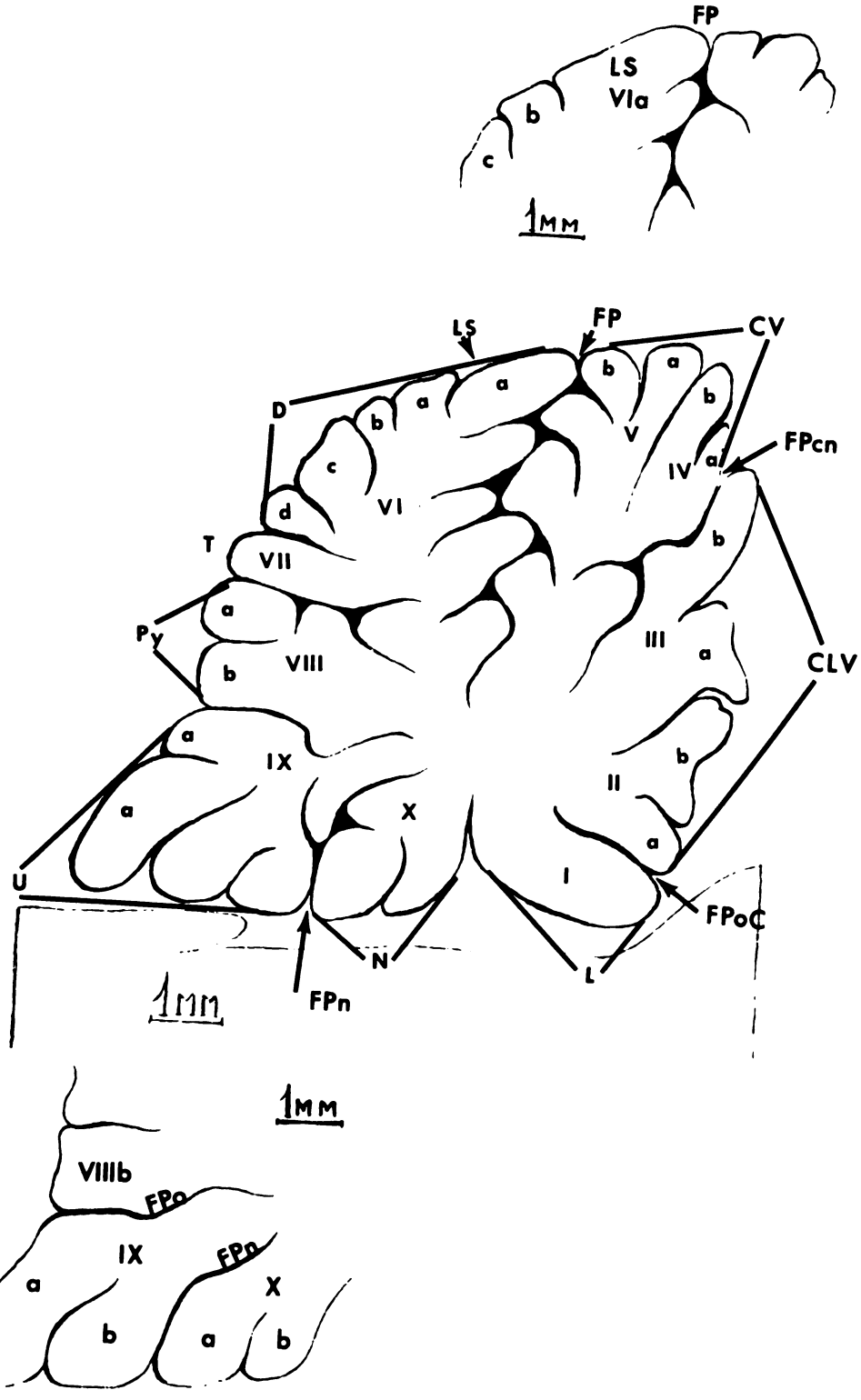


Figure 6. Mid-sagittal view of the cerebellum of the tree shrew *(Tupaia glis)*. The upper inset shows the variation of the lobus simplex seen in *T. chinensis*. The lower inset shows the variation of the uvula and nodulus also seen in *T. chinensis*. See text for discussion.

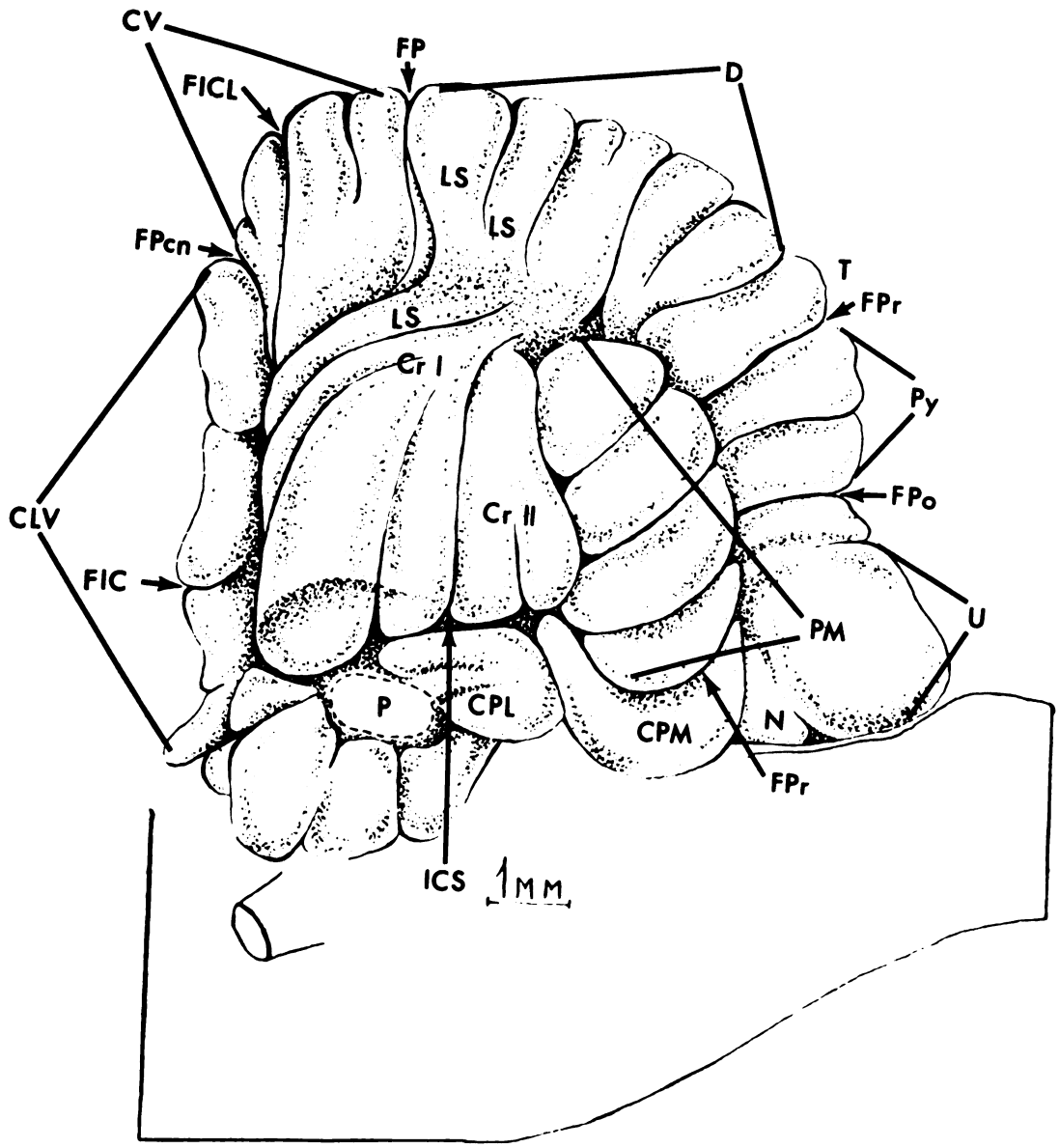


Figure 7. Lateral view of the cerebellum of the tree shrew *(Tupaia glis)*. The paraflocculus (P) has been removed for sake of clarity. Ansiform lobule crus II is partially divided by a shallow sulcus in *T. glis*, however it is usually a single wide folium in *T. chinensis*.

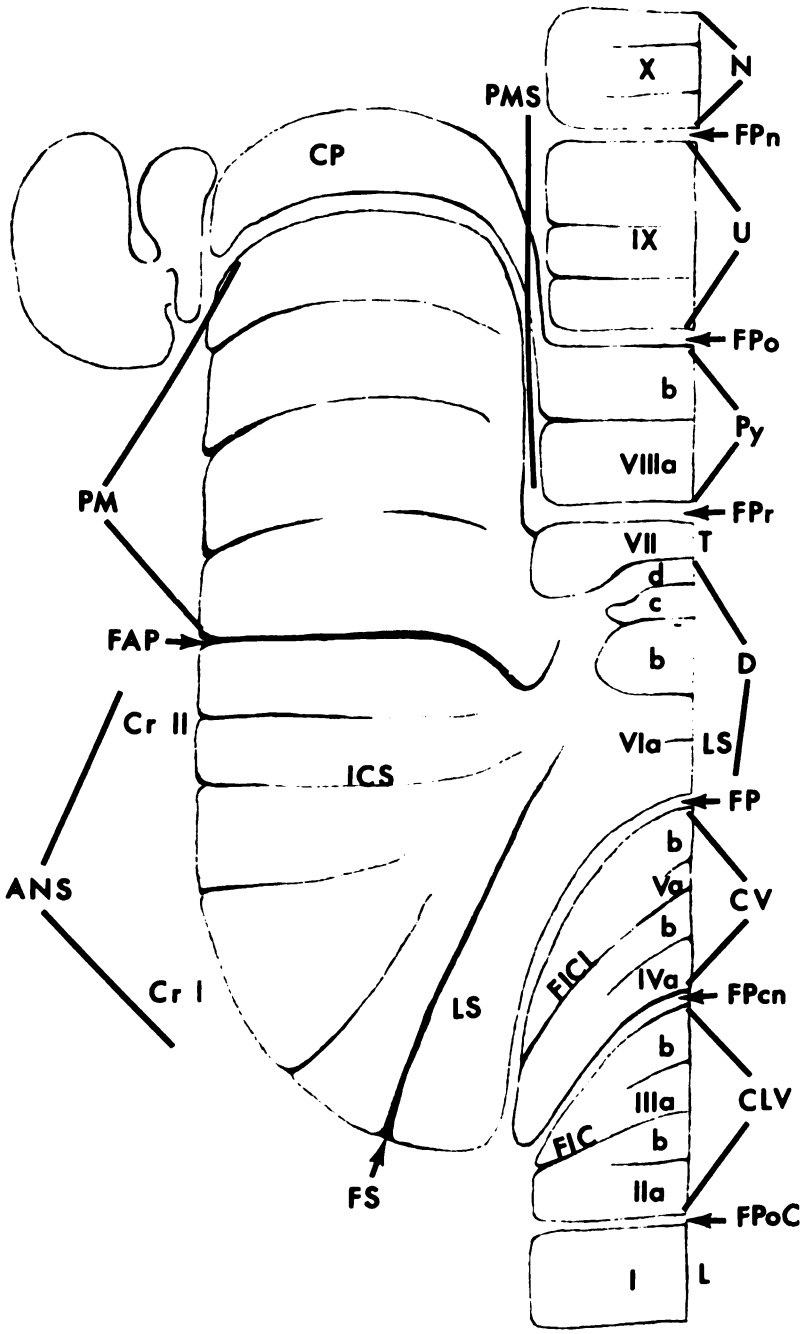


Figure 8. A semi-diagrammatic drawing of the cerebellar cortex in the tree shrew *(Tupaia glis)*. Note particularly the anterior lobe, and the ansiform lobule. This drawing represents those portions of the cortex that are superficially visible, and it is longitudinally flattened so the entire cortex is illustrated on one plane.

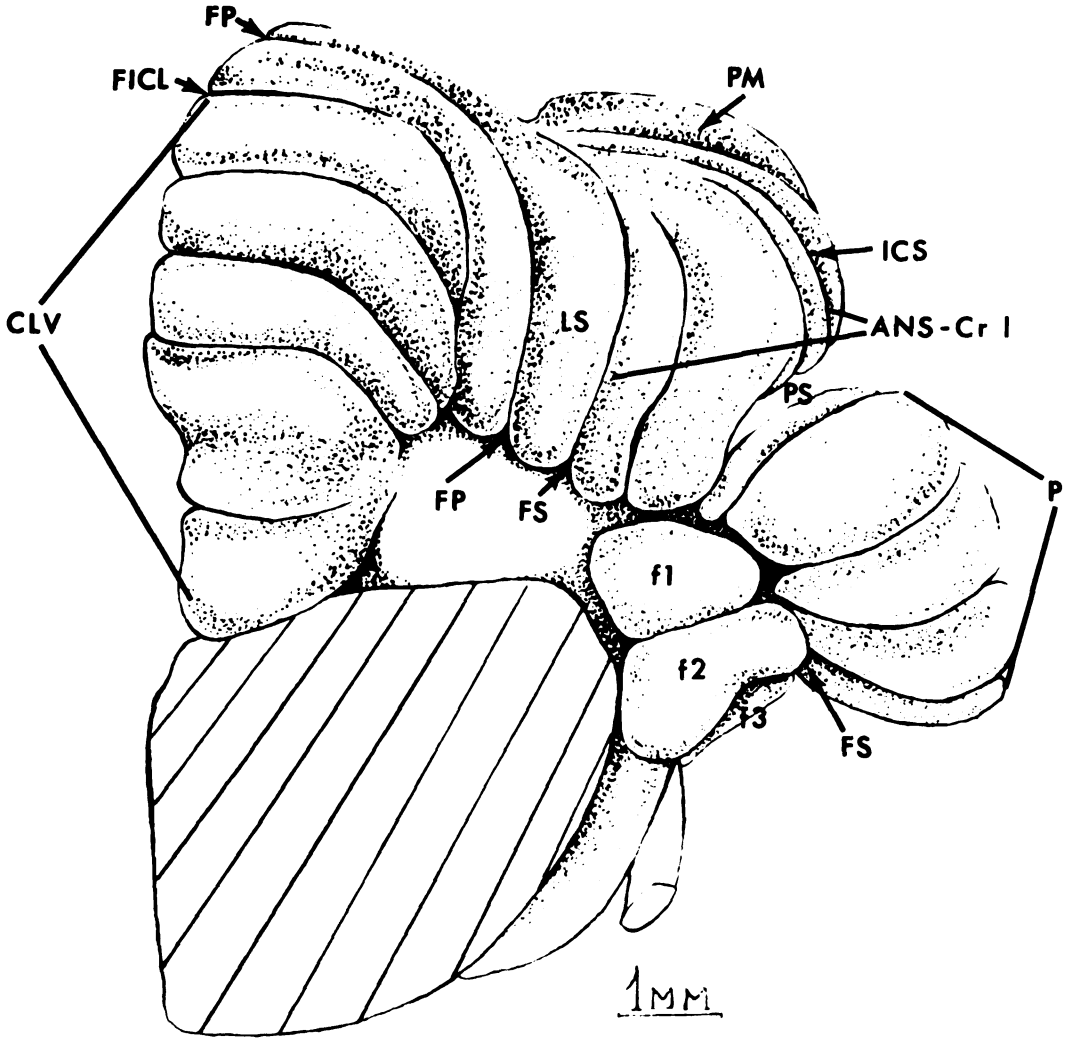


Figure 9. Anterior view of half of the cerebellum of the tree shrew *(Tupaia glis)*. Note the relatively large size of the paraflocculus.

CORRELATIVE DISCUSSION

When contemplating the morphology of the prosimisn cerebellum one is particularly aware of the fact that animals not closely related to primates on the phylogenetic scale, such as cats and dogs (Reighard and Jennings, 1940; Miller *et al.*, 1964) and especially the cetacean (Jansen, 1950), possess a cerebellum of rather complex development. On the other hand many of the lower primates have a rather simple cerebellum. To amply explain the differences would involve a study of the olive, vestibular nuclei and pontine nuclei and spinocerebellar tracts, which is beyond the limits of the present study. Elliot Smith (1903a) was of the opinion that the development of the cerebellum depended on the activities of the animal as well as its zoological rank.

In a series of classical stimulation and lesion studies of the cerebellum, Mussen (1967) attributed general functions to specific regions. The pyramidal lobule functioned in the proper maintenance of backward balance, while the culmen and central lobules are responsible for forward balance. A lesion of the pyramidal lobule would cause the animal to fall backward when it attempts to assume an erect posture. A lesion of the culmen and central lobule would result in the animal running into things or falling forward. Brodal (1967) has shown that the dorsal and ventral spinocerebellar tracts project almost exclusively to the culmen, central lobule and lingula, the pyramidal lobular and to the paramedian lobule to a limited extent. Oscarsson (1965) has shown that the dorsal spinocerebellar tract as well as the

cuneocerebellar tract terminate in the intermediate region of the ipsilateral anterior lobe, with some terminations in the adjacent cortex of the vermis. According to Mussen (1967) using a stimulation technique on the paramedian lobule these ascending fibers are specifically localized to certain lobules. "The dorsal lobule is concerned with movements of the shoulder, the middle lobule with the musculature of the upper leg and the ventral lobule with the activities of the foreleg and paw." The irregular movements in these lesions studies were seen in the cat, and seen ipsilateral to the lesion (Mussen, 1967).

In the overall comparison of the gross topography of the *Galago* and *Tupaia* cerebelli (exclusive of the flocculus and paraflocculus) several significant differences are noted. The anterior lobe of *Tupaia* is entirely vermal in its location while the same area in the *Galago* has relatively large lateral extensions. The pyramidal lobule of *Tupaia* consistently has two folia and the pyramidal lobule of *Galago* has three folia. For the *Galago* this is interpreted as advanced development not only because of the extra folium, but because the pyramidal lobule occupies considerably more of the posterior lobe in *Galago* than in *Tupaia*. If the work of Mussen (1967) on the cat can be extrapolated to the prosimian, the following explanation is offered. The anterior lobe of the cerebellum and the pyramidal lobe are responsible for forward and backward balance respectively. In its mode of locomotion the *Galago* needs a keen sense of balance, whereas the *Tupaia* has little need for such a keen sense since it is quadrapedal. In the rat, which progresses much as the *Tupaia*, there are

lateral portions of the central and culmen lobules, however in this animal the vermal portions of these lobules are not as highly differentiated as in the *Tupaia* (Larsell, 1952; Zeman and Innes, 1963). Furthermore the pyramidal lobule of the rat is composed of one folium, while in *Tupaia* there are two, and in *Galago* three. In a study of fourteen different groups of insectivores representing both "basal" and "higher" forms (Stephan and Andy, 1964) Le Gros Clark (1932) noted that either the pyramidal lobule is a single folium, or it is not even differentiated (by a dividing fissure or sulcus) from the other more rostral portions of the posterior lobe. In these forms the anterior lobe is also poorly differentiated. The advanced development of the anterior lobe and pyramidal lobule of the *Galago* over the *Tupaia* is interpreted as primary traits (anatomy) resulting from a demand upon the animal (i.e. *Galago*) by its environment. This is a type of adaptive radiation (Buettner-Janusch, 1966) in which a primary trait (those portions of the cerebellum predominately related to locomotion) undergoes modification in order for the animal to adequately adapt to a changing environment. In *Tupaia* these adaptive changes apparently did not take place. Therefore this animal is relegated to a state of quadrapedal locomotion with an inability to assume a stable erect posture or progress with great space encompassing leaps as does the *Galago*. To further corroborate this interpretation of the anterior lobe in *Galago* and *Tupaia*, the same lobes in *Tarsius* are noted. The *Tarsius* inhabits arboreal regions of "secondary growth" and progresses by strong, powerful leaps in both horizontal and vertical

directions (Hill, 1955). According to Woollard (1925) the hemispheric portions of the culmen and central lobule extend laterally and come into close apposition to the flocculus, very similar to the condition seen in the *Galago*. From this comparison it can be seen that in prosimians the development of the anterior lobe is possibly, in part, related to locomotion.

A second region deserving a special morphological comparison is the ansiform area crus I and crus II. In the *Galago* the ansiform lobule is composed of only two folia, while in *T. chinensis* it is made up of four folia and in *T. glis* of five. In the *Tupaia* of this study the entire hemisphere rostral to the ansoparamedian fissure is the ansiform lobule. The same region of the hemisphere in *Galago* includes the central lobule pars lateralis, culmen pars lateralis, and ansiform lobule. It has been previously suggested that the expanded anterior lobe in *Galago* is directly related to locomotor pattern; now an explanation is fought for the large ansiform lobule in *Tupaia*. The ansiform lobule in higher mammals, especially higher primates, and man is greatly expanded taking up a large percentage of the cerebellar hemisphere (Crosby *et al.*, 1962). In the cat (Brodal, 1940a) it has been shown that the dentate nucleus (lateral nucleus of Flood and Jansen, 1961) projects to the entire ansiform lobule. It has also been shown (Brodal, 1940b) that the ventral lamina of the principle olivary nucleus projects to the ansiform lobule crus II and the dorsal lamina projects to crus I. A second region projecting to the ansiform lobule is the area of pontine nuclei. In the cat and rabbit these

projections pass to the entire ansiform lobule and to most of the paramedian lobule (Brodal and Jansen, 1946). A third nuclear region of the brain stem projecting directly to the cerebellum is the vestibular nuclear masses. However fibers from the vestibular nuclei project to the flocculus, paraflocculus, nodulus, uvula and fastigii nucleus (Brodal and Hoivik, 1964; Brodal, 1967; Carpenter, 1967). It has also been previously noted that there is a direct relationship between the development of the flocculus and the vestibular mechanism, and between the flocculus and the coordination of eye movement. The morphological significance of this will be discussed later (cf Flocculus and Paraflocculus. In the above discussion it has been shown that there is a correlation between the development of the brain stem nuclei and the related areas of the cerebellar cortex (e.g. vestibular, olive, etc.). When considering the evolution of the cortico-ponto and ponto-cerebellar system, the gross development of the pons is a relative indicator of the complexity of this association pathway. Marsden and Rowland (1965) compared the gross development of the pons, olive, and pyramid over a wide range of mammals including the *Loris*, *Lemur* and greater *Galago*. According to Marsden and Rowland (1965) in most sub-primate forms the pons and olive are poorly developed; the olive barely visible and the pons usually pretrigeminal. These authors noticed that in primates, beginning with the *Lemur*, there is a rapid and progressive increase in the size of the pons and olive. In the *Lemur* the pons is 1/4 post-trigeminal, and in adult man it is 2/3 post-trigeminal. The reader should note that the *Lemurs*

are phylogenetically close to *Tupaia*. To adequately answer the question of the advanced differentiation of the ansiform lobule, a study is needed of the pons, olive, and particularly the pontine nuclei. This is considerably beyond the scope of this present study. For the present it is sufficient to point out that those regions of the cerebellar cortex associated with the pontine and olivary nuclei show an advanced degree of development in the *Tupaia*. This implies a reasonable degree of differentiation of the respective brain stem regions, and the possible existence of an advanced cortico-ponto-cerebellar pathway.

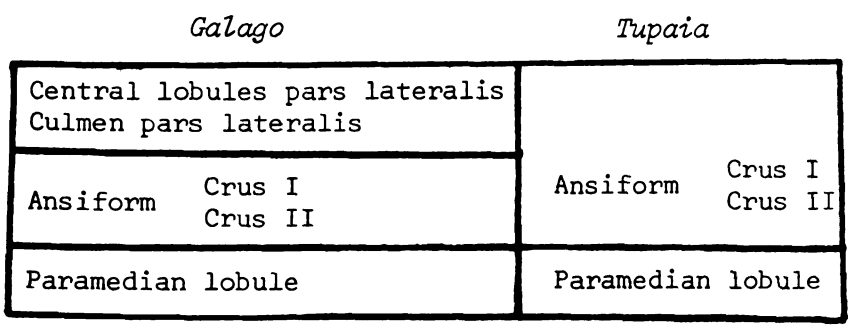
Larsell (1952, 1953) studying the rat and rhesus, and Larsell and Jansen (1967) the avian noticed the relationship between the pubococcygeal muscles and the anterior lobe of the cerebellum, particularly the lingula. Chang and Reich (1949) demonstrated strong projections from the caudal segments of the cord to the lingula in the spider monkey, an animal with a prehensile tail. In *Tupaia* there is a single folium while *Galago* has two folia in the lingula. The tree shrew, because of its quadrapedal mode of locomotion, does not use its tail as extensively for balance as does the *Galago*. The bushbaby in its leaping about and sitting uses its tail extensively for balance. It is the author's opinion that the difference in differentiation of the lingula has been partially governed by the evolutionary development of the locomotor pattern of each animal.

In the *Galago*, sometimes the lobulus simplex is not superficially visible in the vermis and consequently was not given classification

as a sublobule. However at this point, for clarity it will be designated as sublobules VIa with the remaining portions of the declive being sublobules VIb and VIc. This follows the general method of Larsell (1952). Regardless of sublobule classification, the simplex lobule should be called lobulus simplex both in its hemispheric and vermal region (Crosby *et al.*, 1962). The following listing shows the relative comparative complexity of topographical development in *Galago* and *Tupaia*.

Galago		*Tupaia*
Ia, Ib	lingula	I
II	ventral central l.	IIa, IIb
IIIa, IIIb	dorsal central l.	IIIa, IIIb
IVa, IVb	ventral culmen	IVa, IVb
Va, Vb	dorsal culmen	Va, Vb
VIa, VIb, VIc	simplex & declive	VIa, VIb, VIc, VId
VII	tuber	VII
VIIIa, VIIIb, VIIIc	pyramidal	VIIIa, VIIIb
IXa, IXb, IXc	uvula	IXa, IXb
X	nodulus	Xa, Xb

Oddly enough this comparison shows twenty distinct and consistent sublobules for each animal on a mid-sagittal section. A diagrammatic comparison of the cerebellar hemispheres of *Tupaia* and *Galago* follows.



Two anatomical criteria are suggested as evidence for the approximation of *Tupaia* to the primates; [1] the overall complexity of topographical differentiation, and [2] the advanced differentiation of the ansiform lobule. It is this investigator's opinion that these two factors indicate primate tendencies with a rather distinct advancement over the Insectivores. This conclusion is also drawn when comparing *Galago* and *Tupaia*. Perhaps this is a step toward answering the question of Hoffman (1964) concerning increased development of the prosimian cortico-ponto-cerebellar system. "With reference to the increased size (quantitative) of the cerebellum: Is this increase in the cerebellum particularly associated with an increase in the cortico-ponto-cerebellar system with the largest increase in the cerebellar hemispheres and systems through the superior cerebellar peduncle?"

The problem with the term secondary fissure has been discussed. Shortly after its introduction in prosimians by Elliot Smith (1903a) Bradley (1904) suggested that the term had no inherent significance. Larsell (1952, 1953) pointed out that the fissura secunda is the fourth to appear embryologically and therefore the term does not indicate sequence, nor is this fissure necessarily the second deepest.

Furthermore there is disagreement in the literature on what fissure is the "fissura secunda". It is therefore strongly suggested that this term be replaced by the term postpyramidal fissure as previously proposed in this study. The latter term has merit if for no other reason than its descriptive quality.

FLOCCULUS AND PARAFLOCCULUS

GENERAL INTRODUCTORY REMARKS

The flocculus and paraflocculus are phylogenetically some of the oldest parts of the cerebellum, even though in some lower forms they are almost grossly imperceptible (Nieuwenhuys, 1967). In the structurally simple mammalian cerebellum (rat - Larsell, 1952) the flocculus develops from a band of cortex directly associated medially with the nodulus of the vermis, and the paraflocculus developes from the cortex that is medially associated with the uvula (ventral paraflocculus) and pyramid (dorsal paraflocculus). In the adult animals used in this study no distinguishable dorsal and ventral paraflocculi are noticed. Consequently there is no lateral continuation of the postpyramidal and prenodular fissure. There are two possible explanations for no lateral extension of the postpyramidal fissure. First, it could be so poorly developed in the embryo that it readily disappears in the adult, or secondly, since there is no grossly distinguishable dorsal and ventral paraflocculus in the adult this region could have a different sequence of embryological development than the analogous region in the rat (Larsell, 1952).

Stroud in 1895 designated the terms flocculus and paraflocculus, whereas two years later Ziehen referred to these collectively as the floccular lobe (Bradley, 1904). Elliot Smith (1902a, 1903a) also applied the term "lobus flocculi" to both of these regions. Bradley (1904) however, stressed the importance of separate terminology and advocated the use of the terms flocculus and paraflocculus.

Subsequent investigators use this separate terminology.

The flocculus and paraflocculus of the *Galago* and *Tupaia* are considered separately from the rest of the cortex so that they can be discussed in detail with a minimal amount of confusion. It must always be kept in mind that these regions are an integrated part of the cerebellar cortex. Because of its intimate anatomical relationship the copula pyramidis forms an important part of the following discussion.

GALAGO SENEGALENSIS

The flocculus and paraflocculus are the most lateral portions of the cerebellum and the paraflocculus is encased in bone. The flocculonodular portion of this complex composes the archicerebellum, or the vestibulocerebellum (Brodal, 1967).

Flocculus

The flocculus of the *Galago* is made up of four folia (Fig. 4 - p. 36, 10) three of which are incompletely separated from each other. The uppermost folium bulges rostrally, becomes constricted under the stalk of the paraflocculus, and fades out as a narrow band of grey matter passing under the copula pyramidis (Fig. 4 - p. 37). This upper folium is always separated from the remainder of the flocculus by a shallow, yet consistent sulcus. The other two sulci dividing the remaining three folia are essentially intrinsic (Fig. 10). There is a certain amount of variability in the gross structure of the flocculus. To explain this as succinctly as possible the folia of the flocculus are designated f1, f2, f3, and f4 from upper rostral to caudal

(Fig. 10, 11). Folia f1 and f2 vary in size, relative to each other, with f2 usually being the larger. Folium f4 occasionally is merely a narrow slip of cortex, subsequently folium f3 is always the largest of the flocculus (Fig. 4 - p. 37, 10). The flocculus is separated from the paraflocculus by a deep non-descript groove labeled as the floccular fissure by Le Gros Clark (1932). This cleft is acknowledged in the *Galago* (Fig. 10, 11), however the reason for a specific terminology for this cleft is questionable. The flocculus is directly applied to the lateral surface of the brain stem (and cerebellum), while the paraflocculus is located in an osseous fossa. Therefore the bony ridge of the osseous parafloccular fossa is a decisive and natural boundary.

Paraflocculus

The paraflocculus of the *Galago* is affixed to the lateral side of the cerebellum by a medullated stalk (Fig. 4 - p. 37, 12). The folia making up the paraflocculus collectively form a slight medially concave structure (Fig. 12). There are five main folia composing the paraflocculus and these are designated p1, p2, p3, p4, and p5 from rostral to caudal (Fig. 10, 12). Folium p1 is occasionally subdivided by a shallow incomplete sulcus into a larger medial portion and a smaller lateral portion. This is interpreted as a variation in folium p1 based on the location and extent of this intrinsic sulcus (Fig. 10, 11, 12). The sulci between the remaining folia are so deep that the medullated substance of the paraflocculus is visible when these folia are separated. When viewing the paraflocculus from its

dorsal and ventral surfaces the characteristic number of folia are noticed. An additional folium closely associated with the paraflocculus stalk is seen on the ventral view (Fig. 12-B). This is a small, low folium that extends onto the paraflocculus stalk, and has no dorsal counterpart. Folium p4 projects caudally in a rather distinct manner. No dorsal and/or ventral paraflocculus can be distinguished in the adult *Galago* even though these probably occur in the embryological state. A groove is present on the ventral surface of the paraflocculus, and from its position the dorsal and ventral contributions to the paraflocculus can be suggested. If the parafloccular stalk were divided in the middle and the division extended throughout the course of the parafloccular groove (dotted line Fig. 12-B) the paraflocculus would be divided into three rostral (upper) folia and two ventral (lower) folia. The three upper folia (dorsal paraflocculus) are p1, p2, and p3, and the lower folia are p4, p5 and the stalk folium. It must be emphasized that this suggestion is based solely on the adult, and confirmation or dismissal of this opinion must await the study of embryological material. The deep cleft separating the paraflocculus from the lateral hemisphere has been termed the parafloccular fissure by Le Gros Clark (1932) (Fig. 11). It should be noticed that this groove is filled by the dorsal edge of the osseous fossa of the paraflocculus.

The paraflocculus is attached to the cerebellar hemisphere by a short stalk of fibers. Directly surrounding the stalk is a nondescript region of grey matter (Fig. 4 - p. 37). This low region of

cortex is very limited in its extent in most cases. Adjoining this limited region of grey matter is an elevated ridge coming from the copula pyramidis (Fig. 4 - p. 37, 12-A). (This ridge is indicated by a small r in all figures.) By way of this distinct ridge from the copula onto the stalk of the paraflocculus the continuity of these two structures is obvious. In the *Galago* the copula extends further laterally than any other part of the cerebellar hemisphere. As the cortex of the copula becomes the ridge joining the circumpeduncular grey, it proceeds rostrally and turns slightly medially (Fig. 4 - p. 37, 12-A). This lateral appearance of the copular ridge and its continuation with the parafloccular stalk is characteristic for the *Galago*.

Copula Pyramidis

It has been previously stated that what appears to be the lower most folia of the hemisphere in *Galago*, is in fact the copula pyramidis. (For a definition of that portion designated as copula see p. 10.) A caudal and slightly ventral view of the left hemisphere shows the characteristic appearance of the paraflocculus, copula, paramedian lobe and the last three main portions of the vermis (Fig. 13). The copula is distinctly visible from the lateral copular ridge until the cortex extends into the prominent paramedian groove (or sulcus) (Fig. 14). Portions of the paramedian lobule were removed and the pyramidal, uvular, and nodular lobule of the vermis retracted to show the entire lateral-to-medial relations of the copula (Fig. 14). The copula has usually one or occasionally two intrinsic sulci which run

horizontal to its long axis. The intrinsic sulci of the pyramidal lobule stop within the gross limits of this lobule and are not continuous with sulci of the copula. The continuation of the copula into the pyramidal lobule is relatively wide and flat with medullary substance clearly visible at the junction (Fig. 14). Elliot Smith (1903a), when he originally described the copula pyramidis, considered the structure significant, however later concluded that it had little significance (Elliot Smith, 1903b). This study reveals that perhaps his earlier opinions were more accurate. Kanagasuntheram and Mahran (1960), in a study of the gross anatomy of the nervous system of the lesser bushbaby, erroneously stated "...the copula pyramidis which is hidden from the surface by the lateral portions of the middle lobe." Krishnamurti (1966), in a study of the brain of the slow loris *(Nycticebus coucang)*, stated "...the copula pyramidis, a part of which could be seen on either side of the vermis and the rest of it is hidden from the surface by the lateral portions of the middle lobe." As pointed out above, the copula in the *Galago* is not hidden from view, but is a prominent superficial landmark, therefore the present study is not in agreement with these previous investigators. The copula pyramidis of the *Galago* is usually made up of two folia although occasionally three were present (Fig. 4 - p. 37). Since the prepyramidal fissure is deep, the paramedian lobule appears to be resting on the copula. The intrinsic sulci of the copula extend the entire width of the structure in about half of the specimens. When this is the case, the copula made up what

appears to be the lower most two folia of the hemisphere. The extent of the intrinsic sulci of the copula is somewhat variable and this region merits careful examination before its boundaries are accurately determined, otherwise the copula could be mistaken for lower portions of the paramedian lobule.

The fiber connections of the flocculus and paraflocculus of the *Galago* can best be determined definitively by the utilization of a degeneration technique. In the present study it has been noted that the postpyramidal and prenodular fissures have no lateral extensions. In a series of dissections of several cerebelli, which involved removal of the copula, a direct communication between the flocculus-paraflocculus and uvula-nodule is seen (Fig. 15). The postpyramidal fissure appears to stop since there is not a detectable fissure between the copula and underlying bundle of fibers. If one wishes to consider the anatomical apposition of lthe copula and the fibers of the flocculonodular bundle as the lateral representation of the postpyramidal fissure, this is indicated in figure 15. The band of fibers connecting the flocculus and paraflocculus with their respective portions of the vermis is designated as the flocculonodular bundle (Fig. 15). Fibers that are macroscopically visible enter the bundle from the parafloccular stalk, and the flocculonodular bundle in turn radiates out into the nodulus and the uvula (Fig. 15). In an effort to trace the general direction of these fibers several dissections were completed under dissecting microscope beginning with the flocculus and paraflocculus and proceeding medially.

Fibers from the paraflocculus stalk passed into the white matter of the copula and into the flocculonodular bundle. The fibers from the flocculus entered only the flocculonodular bundle. Both the flocculus and paraflocculus appear to send fibers to both the nodulus and uvula. These preliminary observations naturally need the validation of a degeneration study.

ABBREVIATIONS FOR FIGURES 10, 11, 12, 13, 14, and 15

ANS - ansiform lobule
CLPL - central lobe pars lateralis
CP - copula pyramidis
CPL - culmen pars lateralis
F - flocculus
FF - floccular fissure
FNB - flocculonodular bundle
FP - parafloccular fissure
FPn. - prenodular fissure
FPo. - postpyramidal fissure
FPr. - prepyramidal fissure
G - parafloccular groove
N - nodulus
P - paraflocculus
PM - paramedian lobule
PMS - paramedian sulcus or groove
PS - parafloccular stalk
Py. - pyramidal lobule
r - ridge of copula pyramidis
SF - stalk folium
U - uvula

f1		p1	
f2		p2	
f3	floccular folia	p3	parafloccular folia
f4		p4	
f5		p5	

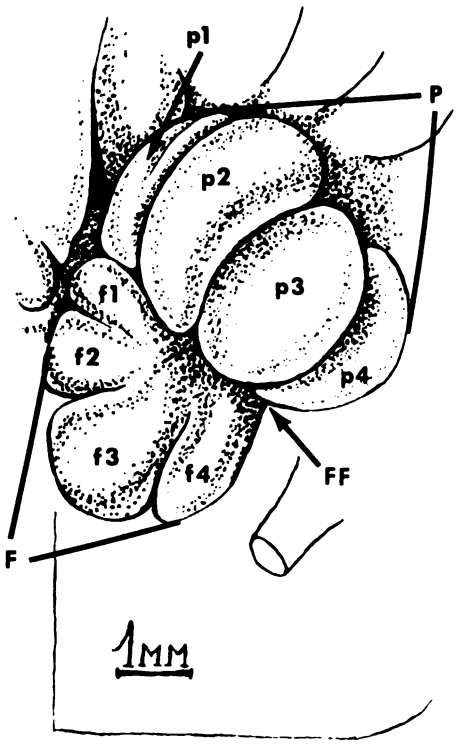


Figure 10. Lateral view of the flocculus and paraflocculus of the lesser bushbaby *(Galago)*. Note the relatively small size of the paraflocculus and the incomplete differentiation of the flocculus.

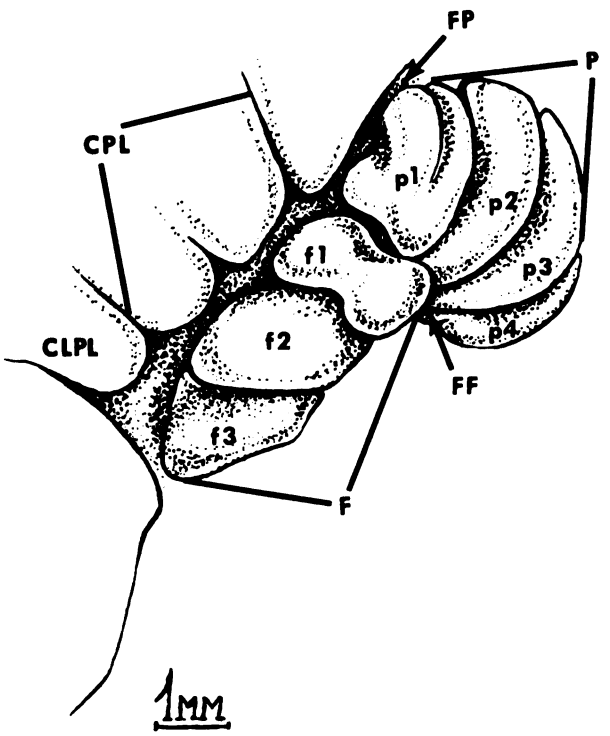


Figure 11. Anterior view of the flocculus and paraflocculus of the lesser bushbaby. Note the intrinsic sulci of folium p1.

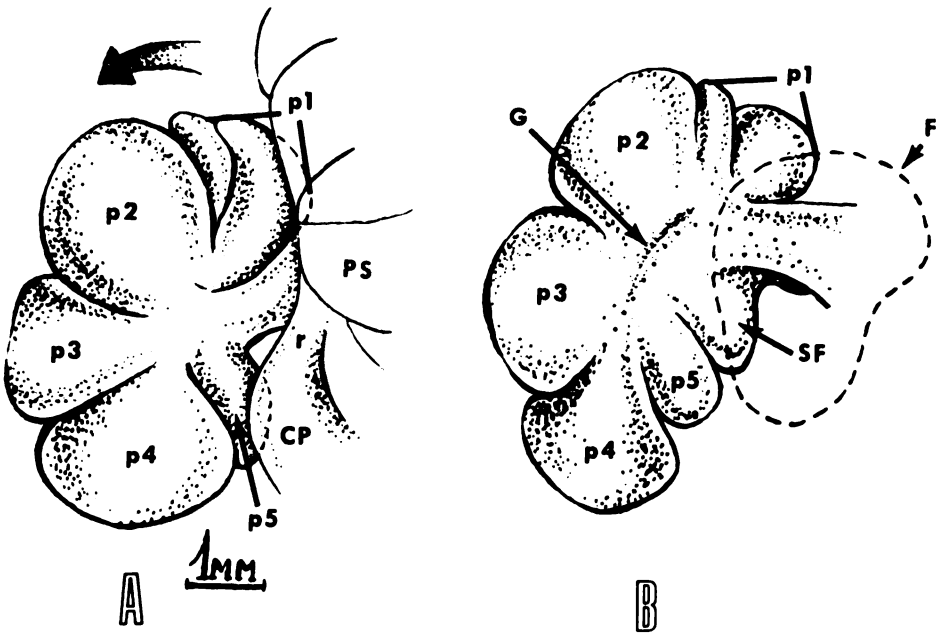


Figure 12. (A) Dorsal view of the paraflocculus of the lesser bushbaby *(Galago)* slightly retracted laterally. Note the lateral extent of the copula pyramidis.

(B) Ventral view of the paraflocculus of the lesser bushbaby *(Galago)*. The oval hashed line (F) represents the relative position of the flocculus. Note the shallow groove, and the theoretical line dividing dorsal and ventral paraflocculi. See text for discussion.

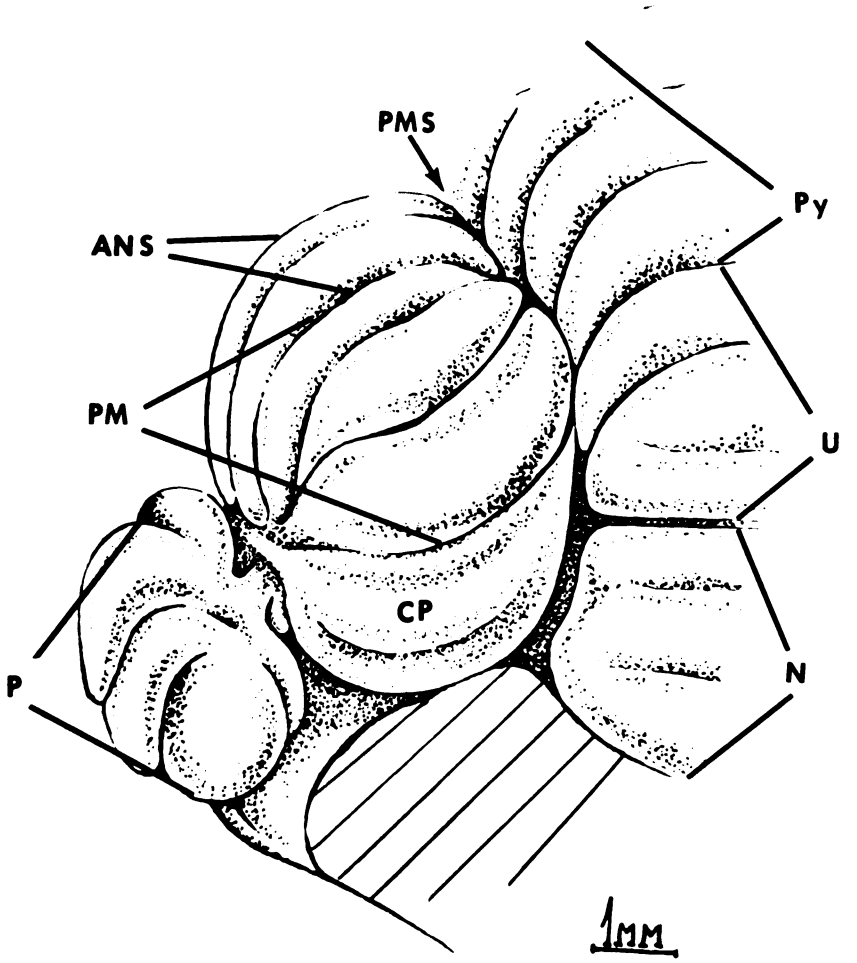


Figure 13. Caudo-ventral view of the left cerebellar hemisphere of the lesser bushbaby *(Galago)*. Note the distinctness of the paramedian sulcus, and the superficially visible extent of the copula pyramidis (CP).

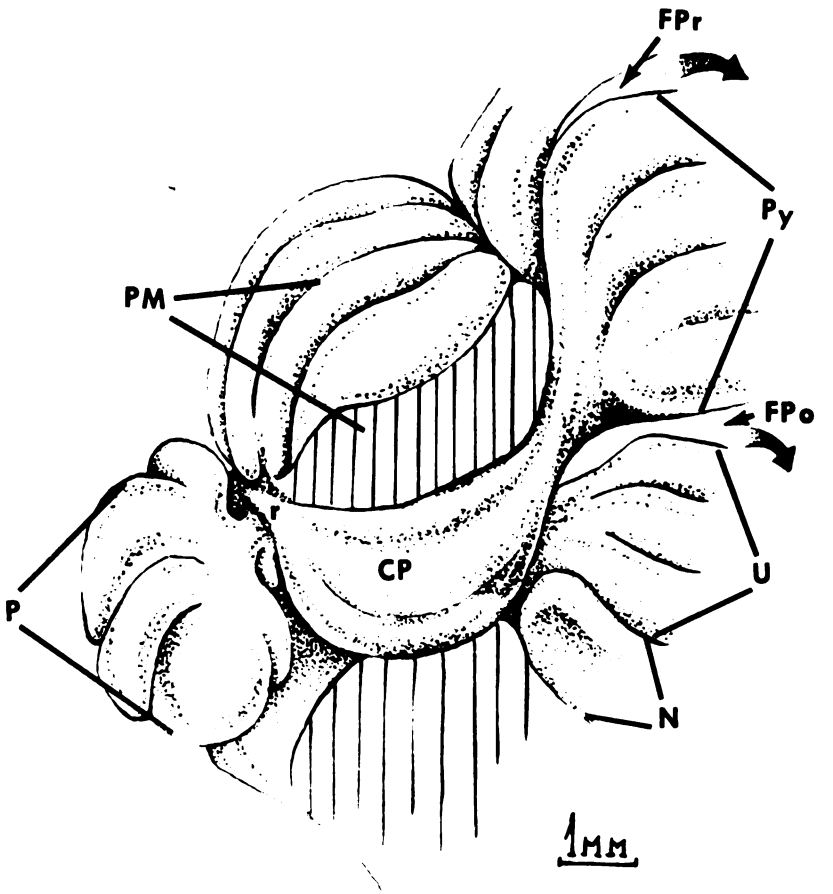


Figure 14. Caudo-ventral view of the left cerebellar hemisphere of the lesser bushbaby *(Galago)*. The lower folia of the paramedian lobule (PM) have been dissected away and the pyramidal, uvular and nodular lobule retracted to show the extent and continuation of the copula pyramidis.

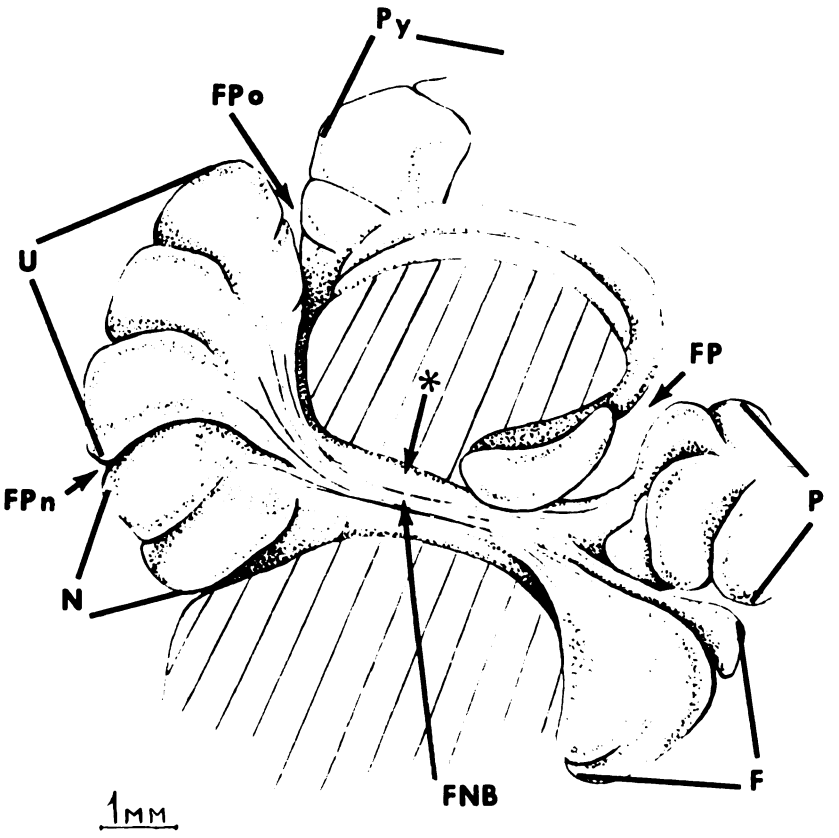


Figure 15. Caudo-ventral view of the right cerebellar hemisphere of the lesser bushbaby *(Galago)*. Most of the copula has been removed, and the paraflocculus and uvular and nodular lobules slightly retracted to show the position of the groove between the F-N bundle and copula pyramidis.

TUPAIA GLIS AND TUPAIA CHINENSIS

The flocculus and paraflocculus of *T. glis* and *T. chinensis* are quite similar in their gross anatomy; therefore the following discussion includes both species. The flocculus and its vermal counterpart, the nodulus, comprise the flocculonodular lobe which, due to its fiber connection with certain vestibular nuclei, compose what has been termed the vestibulocerebellum (Brodal, 1967). The flocculus is directly apposed to the lateral side of the brain stem and cerebellar hemisphere, and the paraflocculus is located in a osseous cavity in the petrous temporal bone. In the pen-tailed tree shrew *(Ptilocercus lowii)* Le Gros Clark (1926) described this cavity as "...a capacious parafloccular fossa." This fossa is not mentioned in his work on the skull of *Tupaia* (Le Gros Clark, 1925).

Flocculus

The flocculus of *Tupaia* is composed of four folia which are distinctly separated from each other by three sulci. These folia are designated f1, f2, f3, and f4, and form a structure long in its horizontal axis (Fig. 7 - p. 50, 16). Folium f1 is occasionally subdivided by a shallow sulcus, while folia f2, f3, and f4 appear to be always undivided. Folium f4 has a narrow buttress of cortex extending caudally upward and under the copula pyramidis lateralis (Fig. 7 - p. 50). As the stalk of the paraflocculus rests on the upper surface of folia f2, f3 and f4 it slightly flattens the dorsal (upper) surface of these lobules (Fig. 19). From an anterior view the flocculus is closely applied to the brain stem and does not "lean" laterally as in

the *Galago* (Fig. 9 - p. 52). The deep groove separating the flocculus from the parafloccular sulcus of Le Gros Clark (1932) (Fig. 9 - p. 52, 16). This groove is also filled by the ventral edge of the osseous parafloccular fossa.

Parafloccular

The parafloccular of *Tupaia* is a relatively large structure, a fact implied by Le Gros Clark (1926), and is made up of six main folia (Fig. 9 - p. 52, 16, 17). These folia are designated as p1, p2, p3, p4, p5 and p6, and collectively form a distinct medial concave structure (Fig. 16, 17). In the medial angle of the parafloccular is a very narrow folium to which the term stalk folium is applied. The five main sulci separating the six folia are very deep and the medullated core of the parafloccular is visible in the valley of each sulcus. A dorsal view illustrates the characteristic appearance and gross configuration of the parafloccular in *Tupaia* (Fig. 17). It is also noted in figure 17 that portions of the ansiform lobule overhang p1 of the parafloccular. In turn, since the parafloccular is quite large in *Tupaia*, folia p1 and p2 invaginate portions of crus I of the ansiform lobule (Fig. 7 - p. 50, 9 - 52, 17). This is the characteristic appearance in both *T. glis* and *T. chinensis*. In the adult *Tupaia* no dorsal and/or ventral parafloccular can be determined. It tentatively appears that folia p1 to p4 form the upper (Dorsal parafloccular) portion and folia p5, p6 and the stalk folium form the lower (Ventral parafloccular) portion. This suggestion is based on a comparison of the parafloccular of *T. glis* and *T. chinensis*. In

T. chinensis the rostral three sulci are at more distinct right angles to the caudal two than the same region in *T. glis*. However this relationship can be seen in the paraflocculus of the latter, it is just less accentuated. This anatomical juxtaposition leaves the observer with the impression that the rostral four folia (p1 - p4) possibly have a different origin than the caudal two folia (p5, p6, and stalk folium). Folium p1 and the stalk folium have intimate topographical relationships with the parafloccular stalk and the copula pyramidis lateralis. The parafloccular stalk is large in the tree shrew and continuous medially with the tear-drop folium of the copula pyramidis lateralis (Fig. 18, 19). The stalk folium passes onto the stalk of the paraflocculus then rapidly diminishes in size. A narrow band of cortex is directly continuous from folium p1 into the cortex of the copula pyramidis lateralis (Fig. 19). Fibers from the stalk of the paraflocculus also enter the white matter of the copula pyramidis lateralis. Thus there is clearly an intimate morphological relationship between the paraflocculus and the copula pyramidis lateralis. The deep cleft between the paraflocculus and the lateral hemisphere is the parafloccular fissure of Le Gros Clark (1932) (Fig. 9 - p. 52). The dorsal edge of the osseous parafloccular fossa extends into this space. In *Tupaia* the copula does not extend laterally, consequently the ansiform lobule is the most lateral portion of the hemisphere.

Copula Pyramidis

In the discussion of the gross topography of the *Tupaia* cere-

bellum it was recorded that what appears to be the lowest folium of the hemisphere is actually the copula pyramidis. In *Tupaia* the copula is differentiated into two distinct and consistent folia, designated, in this study, as the copula pyramidis lateralis and copula pyramidis medialis (Fig. 7 - p. 50, 17). The morphological relationships of the cortex and fibers of the paraflocculus to the smaller of these two folia leave no doubt that it is part of the copula. Directly medial to the smaller folium is a narrow folium extending toward, and into, the paramedian groove. This is the copula pyramidis medialis, and it is directly continuous with the pyramidal lobule. This junction is narrow, and a groove is formed by the manner in which the copula pyramidis medialis joins the pyramid. These two folia collectively form the bridge of cortex that joins the paraflocculus to the pyrmidal lobule, the criterion used by Elliot Smith (1903) to designate the copula pyramidis. In both *T. glis* and *T. chinensis* the copula consists of medial and lateral portions, separated by a moderately deep fissure (Fig. 7 - p. 50). In a study of *Tupaia minor* Le Gros Clark (1924) noted that the copula "...is slightly notched transversly at its lateral extremity...", while in *Ptilocercus lowii* the transverse notch was not present (Le Gros Clark, 1926). It is more significant to note that in a study of a wide variety of insectivora representing "basal" and "advanced" forms the copula pyramidis was consistently observed as being usually wide and always unfissured (Le Gros Clark, 1928, 1932).

The fiber connections of the flocculus and paraflocculus of

Tupaia await illucidation via a degeneration technique. With care, and under a dissecting microscope, gross bundles of fibers can be observed and traced. If the copula pyramidis medialis is removed and the pyramidal, uvula and nodular lobules retracted, a delicate bundle of medullated fibers is seen coursing between the flocculus-parafloccculus and uvula-nodulus complexes. This bundle of fibers is designated the flocculonodular bundle (Fig. 19). Le Gros Clark (1924) reported no grossly observable connections between the flocculus and nodulus in *Tupaia minor*. Larsell (1947a; 1952; 1953) terms this the floccular peduncle in the developing human, rat, cat and monkey. The term flocculonodular bundle is preferred since the term itself is self-explanatory, whereas floccular peduncle is not. The post-pyramidal and prenodular fissures have no grossly detectable lateral continuations. The postpyramidal fissure essentially fades into the nondescript groove between the copula pyramidis medialis and the flocculonodular bundle (Fig. 19). A macroscopic dissection of the fiber bundles beginning in the parafloccular stalk and proceeding medially reveal contributions to the white matter of the copula pyramidis lateralis and medialis and contributions to the flocculo-nodular bundle. Fibers arising in the flocculus pass only to the flocculonodular bundle. This bundle in turn distributes to the uvula and nodulus of the vermis. It is interesting to notice that the flocculus, uvula, and nodulus receive primary and secondary vestibular fibers (Dow, 1936; Carpenter, 1967), therefore the possibility exists that distinct association bundles connect these respective areas and

the paraflocculus. The above mentioned observations on the fibers in the flocculonodular bundle, and the postulation of association bundles merit the validation or refutation of a degeneration study.

ABBREVIATIONS FOR FIGURES 16, 17, 18, and 19

ANS - ansiform lobule
CPL - copula pyramidis lateralis
CPM - copula pyramidis medialis
F - flocculus
FNB - flocculonodular bundle
FPn. - prenodular fissure
FPo. - postpyramidal fissure
FPr. - prepyramidal fissure
FS - floccular sulcus
N - nodulus
P - paraflocculer
PM - paramedian lobule
Py. - pyramidal lobule
SF - stalk folium
U - Uvula

f1	floccular folia	p1	paraflocculer folia
f2		p2	
f3		p3	
f4		p4	
		p5	
		p6	

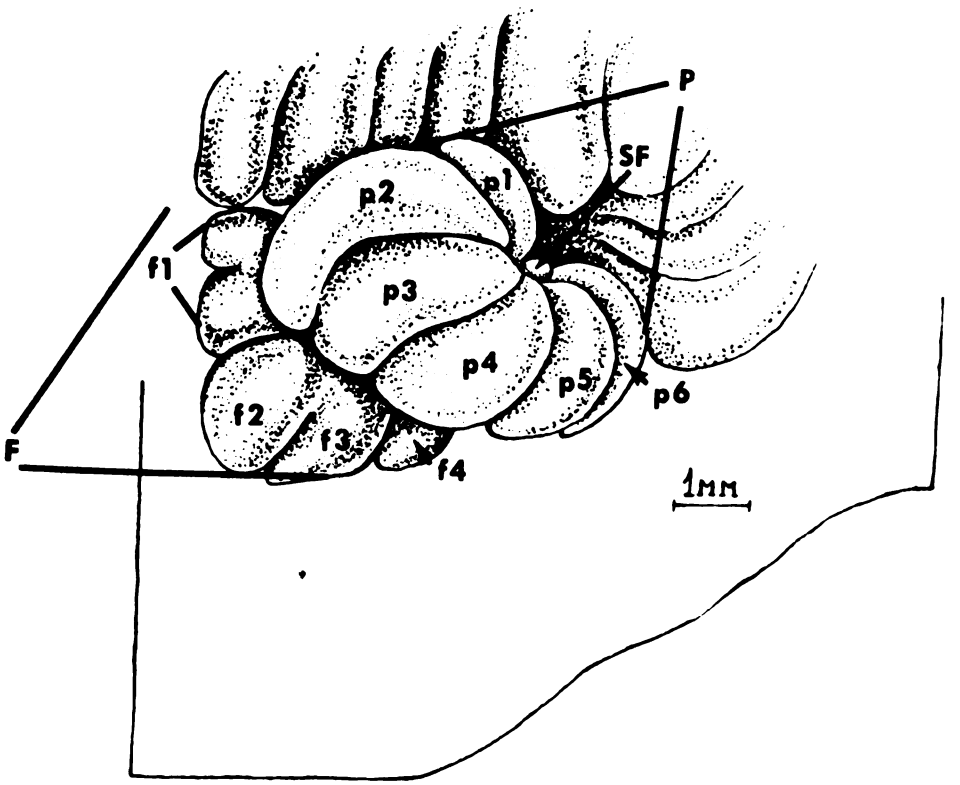


Figure 16. Lateral view of the flocculus and paraflocculus of the tree shrew *(Tupaia glis)*. Note the relatively large size of the paraflocculus, and its medially concave appearance, and the differentiation of the flocculus.

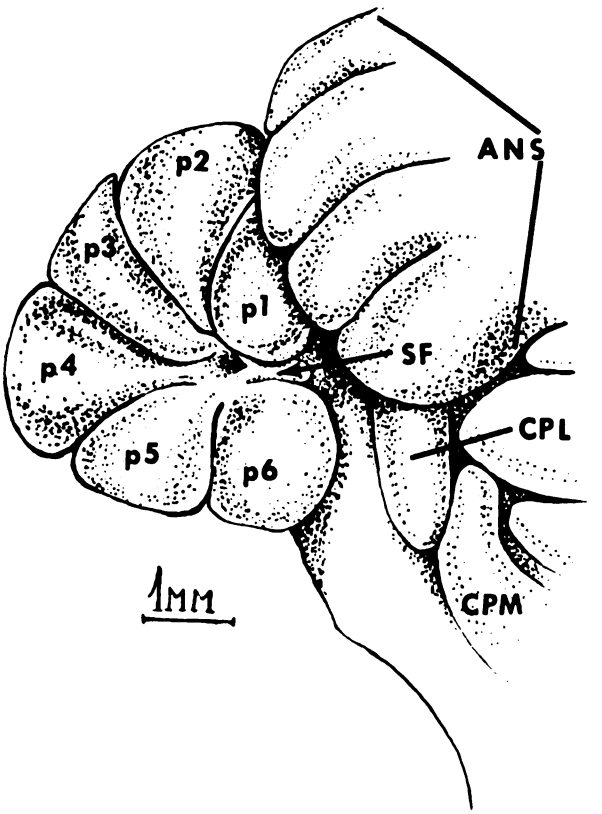


Figure 17. Dorsal and slightly lateral view of the paraflocculus of the tree shrew *(Tupaia glis)*. Note the apposition of the ansiform lobule (ANS) to p1 and p2, and the position of the copula pyramidis lateralis and medialis (CPL-CPM).

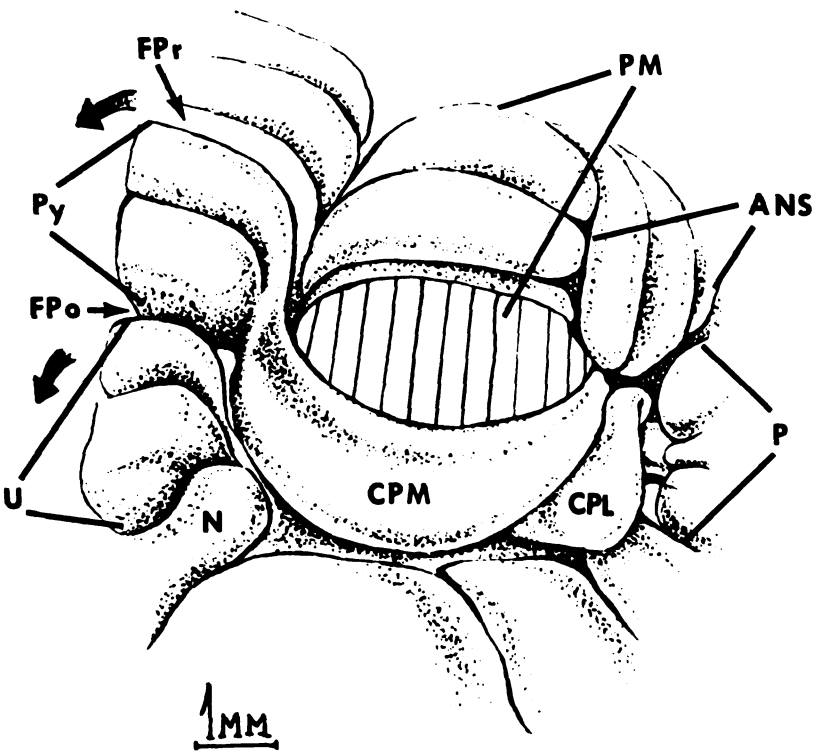


Figure 18. Caudo-ventral view of the right half of the cerebellum of the tree shrew *(Tupaia glis)*. Portions of the paramedian lobe have been removed and the pyramidal, uvular and nodular lobules retracted to show the medial to lateral extent of the copula pyramidis.

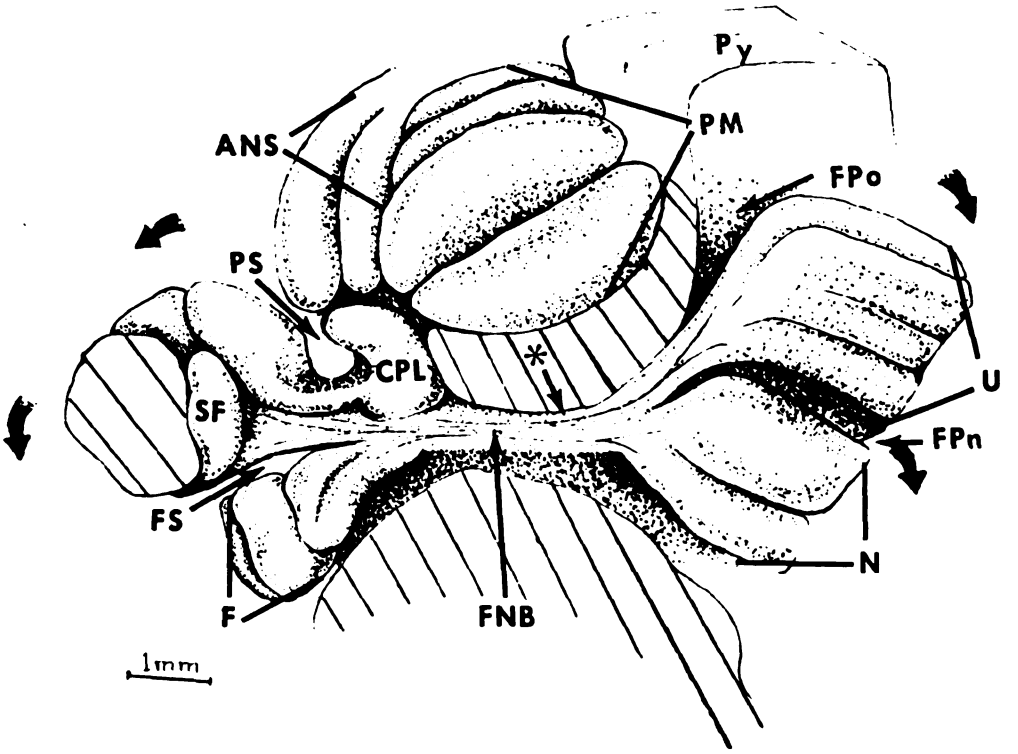


Figure 19. Caudo-ventral view of the left cerebellar hemisphere of the tree shrew *(Tupaia glis)*. The copula pyramidis medalis has been removed and the uvular and nodular lobules retracted to show the position of the flocculonodular bundle. Also note the relationship of pl to the copula pyramidis lateralis. The asterisk marks the position of the groove between the F-N bundle and the copula pyramidis.

CORRELATIVE DISCUSSION

A review of the literature on the gross morphology of the flocculus and paraflocculus of prosimian primates reveals little or no agreement (table I). The observations on the flocculus of the *Tarsius* are particularly striking. It is doubtful that the flocculus of *Tarsius* evolved so rapidly. A similar review of the literature for insectivores reveals less than minimal the available information on the flocculus and paraflocculus in this phylogenetically important group of animals (table II).

The flocculus of the tree shrew and bushbaby are each composed of four folia, with the former being not only more distinctly differentiated into individual folia, but also slightly larger in relation to the remainder of the cerebellar hemisphere. Ariens Kappers *et al.*, (1936) observed that the direct and indirect fiber contributions of the vestibular nuclei to the flocculus undoubtedly play a role in its development. They further observe that flocculo-fugal fibers indirectly effect coordination of eye movements. It is the conclusion of these authors that the degree of eye muscle coordination is directly related to the size of the flocculus in certain mammals (Ariens Kappers *et al.*, 1936). It is a well known fact that the vestibular nuclei send descending fibers to the cord as the vestibulospinal tract and the descending limb of the medial longitudinal fasciculus (Nyberg-Hansen, 1964). The primary ascending fibers from the medial vestibular nucleus form the ascending limb of the medial longitudinal fasciculus and project bilaterally on all nuclei

TABLE I

LITERATURE REFERENCE TO THE PROSIMIAN PARAFLOCCULUS AND FLOCCULUS:

LISTED IN PHYLOGENETIC ORDER ACCORDING TO BUETTNER-JANUSCH (1963.

AUTHOR	ANIMAL	PARAFLOCCULUS	FLOCCULUS
Le Gros Clark 1924	*Tupaia minor*	5 - 6 folia	"few small folia"
Le Gros Clark 1926	*Ptilocercus lowii*	5 - folia	"small"
Elliot Smith 1903a	*Lemur catta*	"irregular mass of folia"	6 - 7 folia
Le Gros Clark 1931	*Microcebus murimus*	2 main folia	3 folia
Krishnamurti 1966	*Nycticebus coucang coucang*	* (3 folia shown in figures)	*
Kanagsuntheram and Mahram 1960	*Galago senegalensis senegalensis*	5 - folia	*
Elliot Smith 1903a	*Tarsius*	5 - 6 bands (folia) with a bifid distal extremity	"bilobulated"
Woolard 1925	*Tarsius spectrum*	* (2 - 3 folia shown in figures)	"minute"
Tilney 1927	*Tarsius*	"large"	"large"

* Not mentioned or discussed.

TABLE II

LITERATURE REFERENCE TO THE PARAFLOCCULUS AND FLOCCULUS OF INSECTIVORES

AUTHOR	ANIMAL	PARAFLOCCULUS	FLOCCULUS
Le Gros Clark 1932	*Centetes ecaudatus*	4 - folia	flattened non-descript cortex
	Microgole	"undivided quadrate"	*
	Erinaceus europaeus	4 - folia	*
	Gymnura rafflesi	"curling upwards and forwards"	"small"
	Blarina brevicauda	"small"	*
	Sorex vulgaris	"small"	*
	Cracidura	3 - folia	"cound not be...identified"
	Scalops aquaticus	3 - folia	"narrow and compressed"
	Talpa europea	"small"	"simple"
	Chrysochloris hottentotta	3 - folia	"small cuboidal folum"
Elliot Smith 1902	*Macroscelides*	*	*
Le Gros Clark 1928	*Macroscelides*	2 - folia	"unfissured"
	Elephantulus	2 - folia	"unfissured"

* Not mentioned or discussed.

of the extrinsic eye muscles (Carpenter, 1967). Carpenter and Strominger (1965) have shown a variety of eye movement defects (paresis) resulting from the interruption of the medial longitudinal fascicules and interruption of fibers projecting to specific nuclei. Woollard (1925) in the *Tarsius* and Detwiler (1939) in *Galago mala* suggest that these animals do not use eye movements to change visual fields, but only move their heads. In *Galago senegalensis* it has been reported (Haines *et al.*, 1968, 1969) that distinct horizontal and vertical ocular movements take place, and that these fine movements are masked by the normal excitable activity of the *Galago*. The incomplete differentiation of the flocculus in the *Galago* is probably related, in part, to this limited amount of ocular movement. In the tree shrew with a more completely differentiated flocculus one would suspect a greater range of eye movement and coordination. From the work of Le Gros Clark (1926) on the position of insertion of the extra-ocular muscles in the pentailed tree shrew, it can be definitely stated that the tree shrew has a potential wide range of eye movement. At this point the correlation is obvious. It must be noticed that range of eye movement is not related to eye coordination. Ariens Kappers *et al.*, (1936) have pointed out that this functional relationship of the flocculus to eye movement is undoubtedly allocated to other areas of the cerebellar cortex in higher primates and man since the flocculi in these animals are small relative to the rest of the cerebellum.

The paraflocculus of *Tupaia* is larger, and consists of one more

folium than the same structure in the *Galago*. Ariens Kappers *et al.*, (1936) proposed, and Brodal and Hoivik (1964) illustrated, primary projections to the paraflocculus of the cat from the vestibular nerve. These are predominately ipsilateral projections. The paraflocculus also receives ipsilateral corticonuclear projections from the lateral part of the dentate nucleus in the cat (Jansen and Brodal, 1940). In a study of the cat, Grant (1962) has also shown that the dorsal paraflocculus receives ipsilateral and contralateral fibers from the dorsal and ventral spinocerebellar tracts. In the rat paraflocculus itself has fiber connections to the flocculus, dentate and interpositus nuclei, lateral portions of the uvula and pyramid, and to the copula pyramidis (Dow, 1936). He found no direct fiber connections from the paraflocculus to the vestibular nuclei. The paraflocculus is therefore an integration center for impulses governing balance and dynamic equilibrium. Based on these facts, it is morphologically clear that both *Tupaia* and *Galago* are relatively well coordinated animals. It is possible that the paraflocculus of *Tupaia* is more differentiated and larger than that of *Galago* to help compensate for the poorer development of the culmen, central lobule and pyramidal lobule. Other implications of this difference in relative development await future study.

The copula pyramidis was originally explained by Elliot Smith (1899a) then later defined by the same author (1903a) as that band of cortex connecting the paraflocculus to the pyramid of the vermis. When distinguishable dorsal and ventral paraflocculi are present this con-

tinuation is between the dorsal paraflocculus and the pyramid. In the *Tupaia* and *Galago* the copula pyramidis is consistently differentiated into separate distinguishable folia; two in the tree shrew and usually two (on occasion three) in the bushbaby. In *Tupaia* the dividing sulcus forms a copula pyramidis medialis (the larger), and a smaller copula pyramidis lateralis. In *Galago* the intrinsic sulci run horizontal to the copula essentially dividing it into upper and lower portions. For the Edentata Elliot Smith (1899a) described this band of cortex as low and flat regardless of the relative complexity of the remainder of the cerebellar cortex. In the opossum, representing a marsupial, Larsell (1936b) described the connection between the paraflocculus and pyramid as a "...fibrous band covered by a thin layer of grisea...", while Obenchain (1925) and Dillon (1963) did not discuss this relationship. In the monotremes Elliot Smith (1899b) and Dillon (1962) did not mention or discuss the copula pyramidis, while Hines (1929) and Abbie (1934) mentioned it only as a narrow constriction joining the myramidal lobule with the paraflocculus. (These last four authors discussed the particular characteristics of the cerebellum of the Monotremata that separate it from other mammalian cerebelli.) The copula in the rat is an unfissured band of cortex (Larsell, 1952). Of primary significance are the observations of Le Gros Clark (1928, 1932) on a variety of Insectivora. He noted that in most instances the copula was a broad band of unfissured cortex. In *Lemur catta* the copula appears moderately fissured (Elliot Smith, 1903a), and this fissuration is advanced in the rhesus

monkey (Larsell, 1953). Since the cat (Larsell, 1953) and the dog (personal observation) also have a foliated copula this development is obviously dependent, in part, on progressive evolutionary changes in the remainder of the cerebellum. However when considering all the diverse types of animals that have a simple copula, the progressive differentiation of this region is considered as a progressive evolutionary change.

With the above discussion in mind the following two criterion are suggested as morphologically relating the *Tupaia* to primates; [1] the decrease in size and differentiation of the copula pyramidis, and [2] the differentiation of the flocculus. The relative largeness of the paraflocculus could be interpreted as an anti-primate characteristic since many sub-primate forms have large paraflocculi.

In the two preceeding main sections the gross topography of the cerebellum of *Galago* and *Tupaia* has been defined. The gross characteristics of the cerebellum of *Tupaia* that relate it to primates has been discussed. Le Gros Clark (1959) has stressed the importance of the total morphological picture, therefore a word is merited on the total brain of *Tupaia*. Stephan and Bauchot (1965) conducted a comprehensive on twenty-seven species of prosimians to determine the "degree of encephalization." This is determined by a comparison of brain and body weights. These investigators noted that the Tupaiiformes show an advanced degree of encephalization. The *Tupaia* have a brain three times as large as the brain of a "basal" Insectivora (e.g., hedgehog, shrews) of equal body size while the Lemuriformes have a brain only twice as

large as a basal insectivora (Stephan and Bauchot, 1965). The Lorsiformes have a brain four times as large as a basal Insectivora of the same body size.

CYTOARCHITECTURE OF THE CORTEX

GENERAL INTRODUCTORY REMARKS

The early perfection of silver staining techniques, and their application to the cerebellar cortex has resulted in this region probably being studied and understood more than any other center (Fox, 1962). The cerebellar cortex is remarkably consistent in its cytologic structure throughout all vertebrates in that it has the same cell types in characteristic relative positions to each other, and the two typical cytologic layers (Nieuwenhuys, 1967; Fox *et al.*, 1967). These layers are the outer molecular layer and the inner granular layer separated by a row of large multipolar neurons, the Purkinje cells. In the molecular layer are the stellate cells, Purkinje cell dendrites, Bergmann fibers, climbing fibers, and parallel fibers; while the main constituents of the granular layer are the granular cells, mossy fibers, and Purkinje cell axons (Fox, 1962). At the junction of these two layers is a row of Purkinje cell bodies closely allied by the Golgi neuron, Golgi epithelial cell, and the Lugaro neuron.

The cytoarchitecture of the cerebellar cortex of the *Galago* and *Tupaia* is essentially identical, and will therefore be considered together. The following discussion is mutually applicable to both prosimians in this study,and the drawings and photomicrographs are taken from both species. Drawings in which the cell bodies are entirely shaded are scale tracings, while those drawings with open cell

bodies are diagrammatic.

The present author is aware of the early and excellent contributions of S. Ramon y Cajal and others to the knowledge of cerebellar cytoarchitecture from 1890-1930. These early studies have been ably summarized in the recent contributions of Fox (1962), Fox *et al.*, (1967). Nieuwenhuys (1967), Eccles *et al.*,(1967), and Larsell and Jansen (1967). For the sake of clarity, conciseness, and to incorporate recent opinions, the studies of these latter authors form the core of the literature used in the ensuing discussions.

GRANULAR LAYER

The granular layer is located between the medullated core of each folium and the Purkenje cell layer. This layer is characterized by [1] cells of small diameter, and [2] a very close organization of the cellular elements with a limited amount of intercellular space. The junction between the medullated core of the folium and the granular layer is somewhat irregular due to an interdigitation of medullated fascicles between the inferior granular cells (Fig. 20). At its junction with the Purkinje cell layer the limitation of the granular layer is clear. The small granular cells invade between the Purkinje cells, but extend no further into the molecular layer (Fig. 20, 21). The thickness of the granular layer is highly variable, from 50 - 400 micra or more. The thinnest regions of the granular layer are in the depths of the fissures where the thickness varies from 50 - 150 micra. The thickness of the granular layer rapidly increases as the summit of a folium is approached. At the summit the thickness ranges

from 200 - 400 micra, or as high as 500 micra. Any depth of the granular layer that exceeds 550 micra in prosimians should be considered excessive and probably represents an oblique section through this region.

The two cell types of the granular layer are the small granular cell and the Golgi cell. The granular cells of the prosimian cortex are 5 - 7 micra in diameter, closely packed, and appear to be little more than a nucleur (Fig. 21). This start appearance of the granular cell is due to a complete lack of Nissl bodies and the thinness of the cytoplasm surrounding the cell body (Fox *et al.*, 1967). It is interesting to note that the measurements of granular cells treated with the Golgi silver method occasionally measured as high as 8 micra, thus illustrating that the rimming cytoplasm in *Galago* and *Tupaia* can attain a total depth of a micra as in the case in *Macaca* and *Saimiri* (Fox *et al.*, 1967).

When subjected to a silver technique the granular cells show the characteristic appearance of their processes, the single ascending axon and several dendrites. The granular cells of the *Galago* and *Tupaia* have 2 - 5 main dendrites with 3 being the most common occurrence (Fig. 22). The main dendrites of the cell terminate as a claw-like ending composed of a series of short extensions, the dendritic digits (Fig. 22, 26). These endings enter into a synaptic relationship with the ascending mossy fiber to form a rosette (Fig. 23). The rosette is made up of specialized segments of the mossy fiber and the dendritic digits of the granular cell. These two fiber components, as well as

fibers descending from the Golgi cell (Fox *et al.*, 1967), make up the fibers of the cerebellar islands, In the luxol fast blue-cresylecht violet stain the cerebellar island stands out as an apparently empty space surrounded by granular cells (Fig. 24). In the silver impregnations the cerebellar islands are represented by the dendritic digits of the granular cells or by clusters of intermingling fibers surrounded by non-impregnated granular cells (Fig. 24-C). Even though the rosette appears to be a solid structure, it is actually a close apposition of a group of highly convoluted fibers (Fig. 23-B). Since the portion of the mossy fiber between successive rosettes is sometimes myelinated, the possibility of the rosette representing a specialization of the node of Ranvier has been postulated (Fox *et al.*, 1967). The second process of the granular cell is the axon, which varies in length considerably (Fig. 25). Regardless of the length of the axon it has three consistent features; [1] it arises either from the cell body or from a dendrite, [2] upon entering the molecular layer it bifurcates into the paralled fibers of this level, and [3] the axon is slender when it arises but usually enlarges in diameter after it bifurcates into the parallel fibers (Fig. 25, 26). These conditions are also seen in the *Macaca* and *Saimiri* (Fox *et al.*, 1967). If the axon arises from the cell body, it exits from any point of the surface of the perikaryon and ascends into the molecular layer. When the axon arises from a dendrite it usually exits from a main ascending dendrite (Fox *et al.*, 1967). In the *Galago* and *Tupaia* granular cell axons are seen to arise from horizontal and on occasion from descending dendrites (Fig. 25-C).

In one instance an axon appeared to arise from a clump of dendritic digits.

The Golgi cell perikaryon is approximately 8 - 12 micra in diameter and collectively these cells are located between or just slightly above the Purkinje cells (Fig. 21). They are recognized by the characteristic appearance of the nucleus, and the presence of fine Nissl bodies, a contrast to the surrounding granular cells. In the silver methods used in the present study the Golgi cells unfortunately did not impregnate and consequently could not be illustrated. The relative position of the Golgi cell and its ramifications is diagrammatically illustrated in Figure 27 (After Fox, 1962; Fox *et al.*, 1967). The dendrites of the Golgi cell ascend in the molecular layer, and its axonic plexus descends into the granular layer to synapse in the rosettes of the glomerular island. The width of distribution of the dendrites in the molecular layer usually correlates with the field of distribution of the axonic plexus of the same cell in the granular layer (Fox *et al.*, 1967). These authors also state that displaced Golgi cells, (i.e., cells located distinctly within the molecular layer) are rare. In the present study some cell bodies that have the general shape of a Golgi cell are noted, however their dendritic distribution is unlike that of the Golgi cells in *Macaca* (Fox *et al.*, 1967). It is also noted that these Golgi-like cell bodies are located above the Purkinje cell, which, according to Fox *et al.*, (1967), is not normal for Golgi cells. At this point these cells are identified as inferior stellate cells of the molecular

layer. It is possible that future study may expose these cells as Golgi neurons. If this proves to be the case, the distribution of their processes is considerably different from the Golgi neurons of the simian cerebellum (Fox *et al.*, 1967).

The fiber components of the granular layer are the processes of the granular cells (Fig. 22, 25), the mossy fibers (Fig. 23), the axons of the Purkinje cells (Fig. 27, 28), the axonic plexus of the Golgi cell (Fig. 27), and the climbing fibers as they extend upward from the medullated core to the molecular layer.

PURKINJE LAYER

The Purkinje cells, located at the junction of the molecular and granular layer, are the main efferent neurons of the cerebellar cortex. These cell bodies are medium sized (18 - 23 micra) and their dendritic ramifications in the molecular layer are always flattened in a transverse orientation to the folia. The Purkinje cell dendrites are therefore studied best in para-sagittal sections. The dendrites of the Purkinje cell arise from the apex of the cell body as a single primary ramus which divides into 2 or 3 secondary rami which in turn terminate as smooth tertiary rami (Fig. 28 A & B). From the tertiary smooth rami terminal branchlets arise which are heavily laden with small spines, the gemmules (Fig. 28-B). A single axon arises from the inferior portion of the cell body and descends into the granular layer where it sends off collateral and recurrent collateral branches. The parallel fibers, the bifurcated axons of the granular cells, enter into a synaptic relationship with the gem-

mules of the terminal branchlets, while the climbing fibers have axo-dendritic synaptic relationship with the secondary and tertiary smooth rami (Fig. 29). The climbing fibers also send collaterals to the superior and inferior stellate cells. The recurrent collateral fibers of the Purkinje axon form supra- and infraganglionic plexuses above and below the Purkinje cell body and are believed to enter into synaptic relationship with the Golgi neurons (Fox *et al.*, 1967). For further detail of these synaptic relationships and the neuronal circuits formed by them, the reader is referred to the monographs of Eccles *et al.*, (1967) and Fox *et al.*, (1967).

A second type of cell in anatomical juxta-position to the Purkinje cell is the intermediate cell of Lugaro (Fox, 1959) (Fig. 30). This cell, indicated as a neuron by Fox (1959) is small (9 - 13 micra) and fusiform in shape. These cells are characterized, in silver sections, not only by their position relative to the Purkinje cell, but also by the fact that its processes spread horizontally from opposite ends of the cell body. Even though these cells lie close to the Purkinje cell body their synaptic relationship is mainly with the "paint-brush" formations of the basket cells, and the perikaryon of the basket cells. It is also felt that processes of the Lugaro cell synapse in the upper regions of the granular layer (Fox, 1959). In the *Galago* and *Tupaia* the processes of the intermediate Lugaro cell enter the molecular layer in an oblique manner, and do not enter into the formation of the pericellular basket, but only approach the axon hillock region (Fig. 30). The synaptic relationship of the Lugaro cell processes to

the inferior stellate cells is also observed (Fig. 30-B).

A third cell type located in apposition with the Purkinje cell is the Golgi epithelial cell (Fox *et al.*, 1967) (Fig. 31-B). The cell body is small (9 - 13 micra) with characteristic ascending processes. These processes arise from the dorsal aspect of the cell body as 2 - 5 main stalks (Fig. 31-B), and ascend through the molecular layer. There are numerous small lateral projections from the main ascending process. Collectively the ascending processes of the Golgi epithelial cell are termed Bergmann fibers (Fig. 31) (Fox *et al.*, 1967). It is interesting to note that in the *Galago* and *Tupaia* these fibers appear to be located between the Purkinje cells. Penfield (1932) suggested that these cells are specialized neuroglial elements, probably a special form of astrocyte. Mugnaini and Forstronen (1965) noticed that the Bergmann fibers are in very close apposition to the Purkinje cells throughout their extent, and suggested that the Golgi epithelial cells serve a nutritional function relative to the Purkinje cell.

The location and processes of the Golgi neuron has been previously discussed (Fig. 27).

MOLECULAR LAYER

The outermost layer of the cortex of the prosimian cerebellum is the molecular layer (Fig. 20). It is made up of a preponderance of fibers (Fig. 32), with a random population of stellate cells; the only intrinsic neuron of the molecular layer. Approximately the lower half of the molecular layer has a dense population of horizontal fibers

(Fig. 32). These are the parallel fibers from the axons of the granular cells, processes of the intermediate cells of Lugaro, Golgi cell processes, and the processes of the inferior (or deep stellate) cells. The molecular layer varies in depth from approximately 150 - 340 micra. There does not appear to be a tendency for the thinnest regions of the molecular layer to be in the depths of the fissures as is the case for the granular layer. The thinnest portions of the prosimian molecular layer are on folia located within the primary fissure.

The stellate cells of the molecular layer are arbitrarily designated as inferior stellate cells, or basket cells, in the lower 1/2 - 1/3 of the layer, and as superior stellate cells in the outer 1/2 - 1/3 of the layer (Fig. 33, 34). The inferior stellate cells are small (11 - 16 micra) and commonly known as the basket cells, The cell bodies of the basket cell send long processes through the molecula layer just above the level of the Purkinje cell bodies. These processes extend in a transverse direction through the folium and are termed the transversal fibers and best visualized in sagittal sections (Fig. 33). The transversal fiber in turn gives off three types of extensions: ascending collaterals, descending collaterals, and longitudinal collaterals that branch at right angles from the transversal fiber (Fig. 33). The longitudinal collaterals extend through the longitudinal axis of the folia, and are best visualized in frontal sections. The descending collaterals surround the Purkinje cell body and synapse primarily on the axon hillock or on the descending portion of the axon of the Purkinje cell (Fig. 35). The synapse usually does

not take place between the Purkinje cell perikaryon and the basket cell processes. In the *Galago* and *Tupaia* of this study the length of the transversal fibers of the basket cell are traced for a distance encompassing 10 - 13 Purkinje cells, and the longitudinal collaterals for a distance of 3 - 5 Purkinje cells. Fox *et al.*, (1967) have observed the transversal fibers extending for a distance of 18 - 20 Purkinje cells, and the longitudinal collaterals for a distance of 6 Purkinje cells.

Scheibel and Scheibel (1954) divided the stellate cells into two categories, [1] those with processes that break up a short distance from the cell body, and [2] cells with long transversal fibers and long longitudinal collateral fibers. These two types of cells are seen in the prosimian cerebellum (Fig. 33, 34). In addition to these categories several other cells are observed in the present study that appear to combine these characteristics reported by Scheibel and Scheibel (1954). A fortunate impregnation permitted the tracing of this type of cell (Fig. 33-B). This stellate cell was always observed in about the middle 1/3 of the molecular layer. Some of its processes are short and break up in the immediate vicinity of the cell body, while there are also several long ascending and descending processes from the cell body. The descending processes extend as far as the Purkinje cell bodies. In addition to these shorter ascending and descending processes, a long transversal fiber is noticed extending for a considerable distance horizontally through the molecular layer. This transversal fiber also gives rise to descending collaterals which

presumably assist in the formation of a Purkinje cell basket (Fig. 33-A). From the results of this study it is possible that there exist a third type of stellate cell. Fox *et al.*, (1967) observed no descending collaterals from the superior stellate cells entering into the formation of a Purkinje cell basket, or a "paint brush" tip (Fig. 35-B). Based on the anatomy of these middle stellate cells it is possible that the synaptic relationship of a superior stellate cell to the Purkinje cell is through this middle stellate cell.

The superior stellate cells impregnate poorly and their specific function is unclear (Fox *et al.*, 1967). In the present study few superior stellate cells impregnated, however tracings were made of some cells (Fig. 33). From the observations made of the superior stellate cells of *Galago* and *Tupaia* it appears that they are stellate cell type 1 as described by Scheibel and Scheibel (1954). It has been pointed out by others (Eccles *et al.*, 1967) that superior stellate cells do have, in some cases, transversal processes. The superior stellate cells and the basket cells have reciprocal synapses with each other. The basket cells in turn synapse on the axon hillock of the Purkinje cell to form the characteristic paint brush tip (Fig. 35). Fox *et al.*, (1967) have shown that the smooth transversal fiber of the basket cell enter into synaptic relationship with the spiny branchlets and dendritic spines of the Purkinje cell. With all of the reciprocal relationships of the axons and dendrites of the cells of the cerebellar cortex the potential circuits are almost innumerable. For a detailed discussion of the excitatory and

inhibitory postsynaptic potentials, and their pathways, and specific cell types believed to initiate an excitatory or inhibitory response, the reader is referred to Eccles *et al.*, (1967).

DISCUSSION

The cytologic structure of the mammalian cerebellar cortex is extremely consistent in its structure, and the *Galago* and *Tupaia* are not exceptions. They show all the typical mammalian characteristics in cell type, size of individual cell types, and the general distribution of specific cell types. The prosimians of this study share with the *Macaca* an irregularity in depth of the granular layer. It was noted in the discussion that Golgi neurons could not be identified, but there appeared to be Golgi-like cell bodies located approximately 50 micra above the Purkinje cells. These cell (tentatively interpreted as inferior stellate cells) bodies appear to be quite similar to Golgi cell bodies described for the *Macaca* (Fox *et al.*, 1967). However the branching pattern of these cells is different from that in *Macaca*, and these cell bodies are always displaced upward into the molecular layer. Fox *et al.*, (1967) stated that displaced Golgi neurons are "...in rare instances in the molecular layer." In the present study these Golgi-like cells are always observed in the molecular layer.

Nieuwenhuys (1967) and Larsell and Jansen (1967) have discussed in some detail the changes that take place at the cytologic level as animals ascend the phylogenetic scale. These changes can be summarized as two main points: [1] the individual cellular elements,

e.g., Purkinje, become progressively more complex in their individual structure, e.g., number of branches and branching pattern, and [2] the cytologic layers become progressively more differentiated into distinct separate layers. Perhaps overshadowing these two points is the fact that grossly the cerebellum is becoming a more prominent segment of the rhombencephalon.

The granular cells of the *Galago* and *Tupaia* cerebellum, in some cases, appear to have axons arising from horizontal and descending dendritic processes. Aside from the two catagories of stellate cells proposed by Scheibel and Scheibel (1954) another type of stellate cell is observed and described in this study. With the exception of these two minor points, the cytoarchitecture of the prosimian cerebellar cortex conforms to that of *Macaca mulatta* and *Saimiri sciureus* so ably described by Fox *et al.*, (1967).

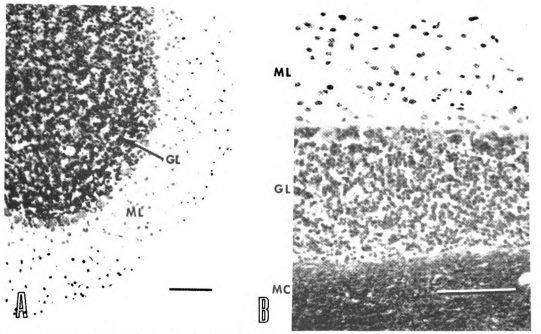


Figure 20. Cytologic layers of the cerebellar cortex of the *Galago* (A) and *Tupaia* (B). Abbreviations: GL = granular layer, ML = molecular, MC = medullated core. Luxol fast blue-cresylecht violet. Scale = micra.

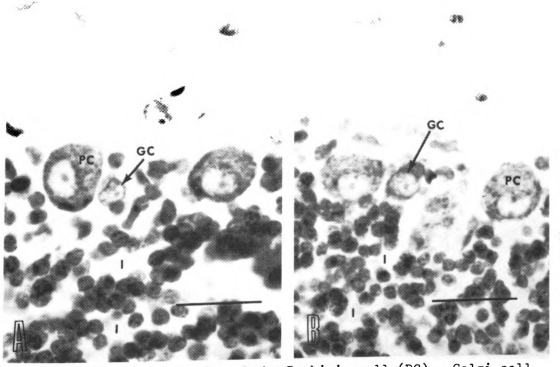
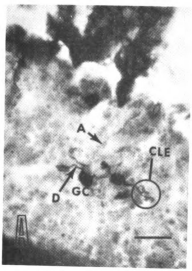
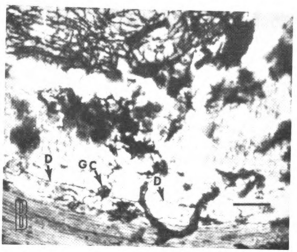


Figure 21. Photomicrographs of the Purkinje cell (PC), Golgi cell (GC), and cerebellar islands (I). Note the appearance of the granular cells. Figure 21-A is *Galago,* 21-B is *Tupaia*. Luxol fast blue-cresylecht violet. Scale = 30 micra.





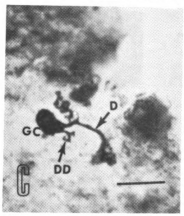
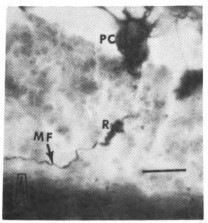


Figure 22. Photomicrographs of granular cells with long dendrites (B) and short dendrites (A,C). Abbreviations: GC = granular cell, D = dendrite, DD = dendrite digit, A = axon, CLE = claw-like ending. Rapid Golgi. Scale = 15 micra.



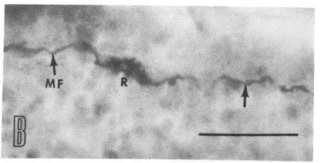


Figure 23. Photomicrographs of a low magnification (A) and high magnification (B) of a mossy fiber rosette. Note that the rosette under high power (B) is not a solid structure, but highly convoluted. Abbreviations: MF = mossy fiber, R = rosette, PC = Purkinje cell with pericellular basket. Rapid Golgi. Scale = 25 micra.

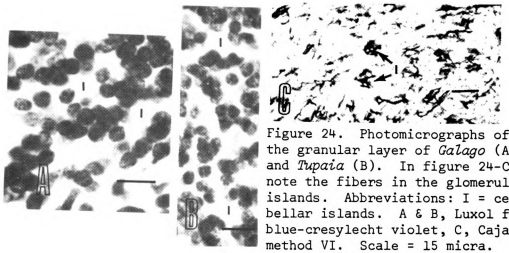


Figure 24. Photomicrographs of the granular layer of *Galago* (A) and *Tupaia* (B). In figure 24-C note the fibers in the glomerular islands. Abbreviations: I = cerebellar islands. A & B, Luxol fast blue-cresylecht violet, C, Cajal method VI. Scale = 15 micra.

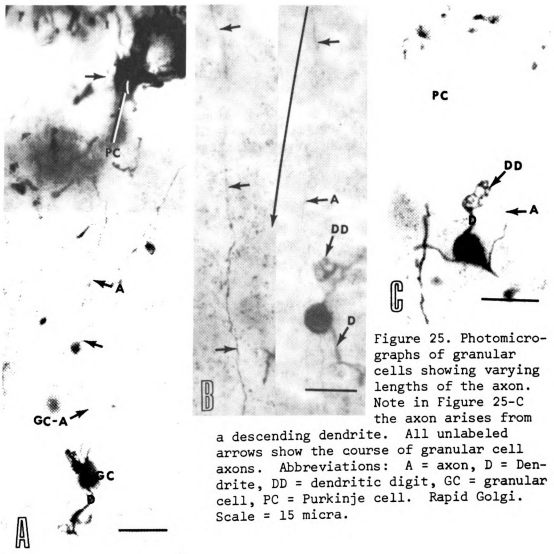


Figure 25. Photomicrographs of granular cells showing varying lengths of the axon. Note in Figure 25-C the axon arises from a descending dendrite. All unlabeled arrows show the course of granular cell axons. Abbreviations: A = axon, D = Dendrite, DD = dendritic digit, GC = granular cell, PC = Purkinje cell. Rapid Golgi. Scale = 15 micra.

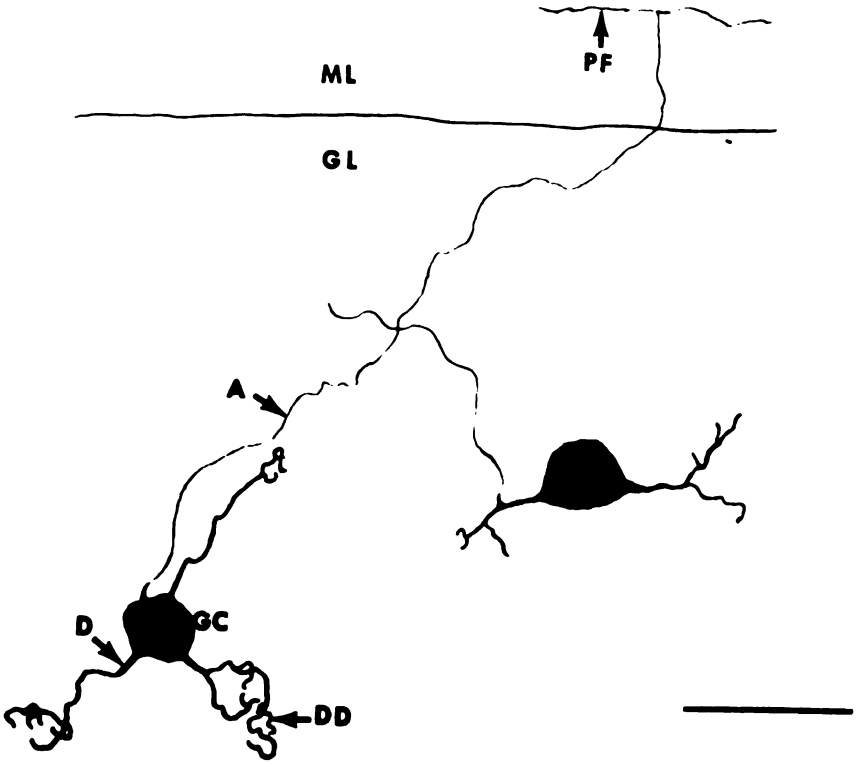


Figure 26. Tracing of granular cells and their processes. Abbreviations: A = axon, D = dendrite, DD = dendritic digit, GC = granular cell, GL = granular layer, ML = molecular layer, PF = parallel fiber. Scale = 15 micra.

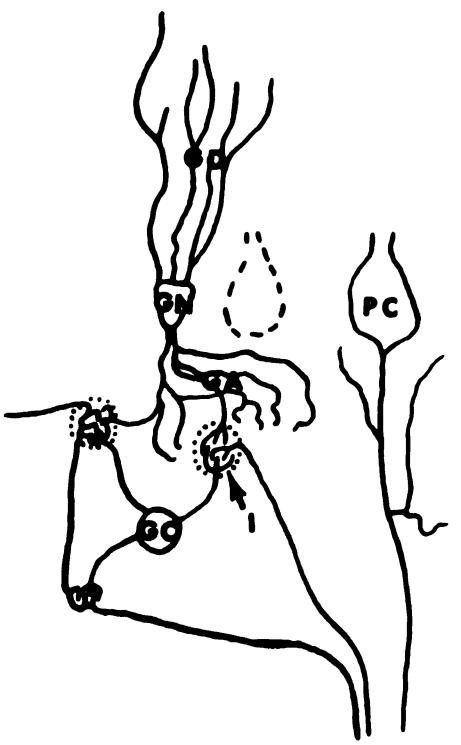


Figure 27. Diagrammatic illustration of the relative position of the Golgi neuron (G N) and Purkinje cell (PC). Abbreviations: GC = granular cell, I = cerebellar island, GD = Golgi dendrites, GA = Golgi axonic plexus.

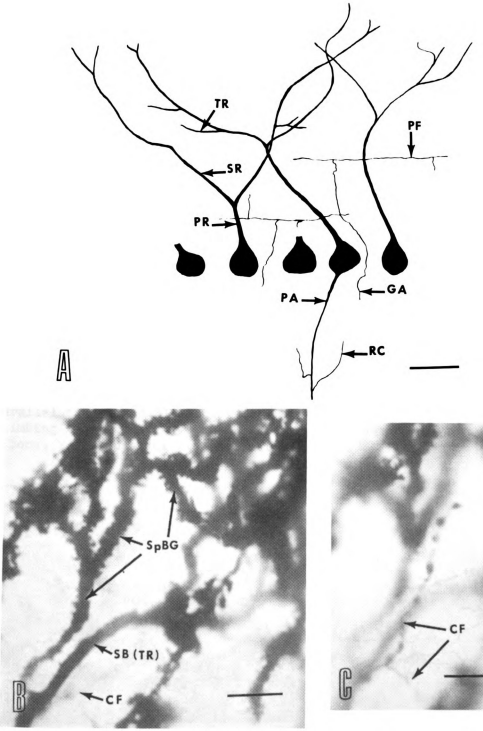


Figure 28. Tracings and photomicrographs of Purkinje cell distribution and terminations. Abbreviations: CF = climbing fiber, GA = granular cell axon, PA = Purkinje axon, PF = parallel fibers, PR = primary rami, RC = recurrent collateral, SB = smooth branches, SpBG = spiny branchlets with gemmules, SR = secondary rami, TR = tertiary rami. Figure 28-C is a different level of focus of B. Rapid Golgi, Cajal method IV. Scale = 30 micra (A), 5 micra (B,C).

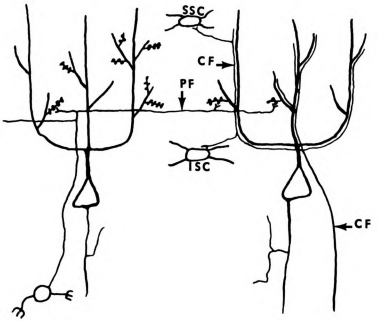


Figure 29. Diagrammatic illustration of the relationship of parallel fibers and climbing fibers. Abbreviations: CF = climbing fibers, ISC = inferior stellate cell, PF = parallel fibers, SSC = superior stellate cell.

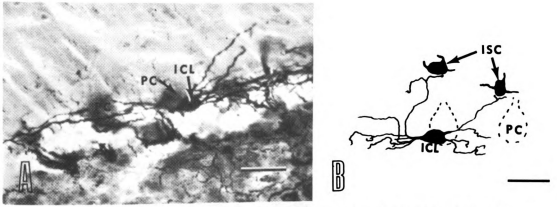


Figure 30. Photomicrograph and tracing of the intermediate cell of Lugaro. Abbreviations: ICL = intermediate cell of Lugaro, ISC = inferior stellate cell, PC = Purkinje cell. Rapid Golgi. Scale = 25 micra.

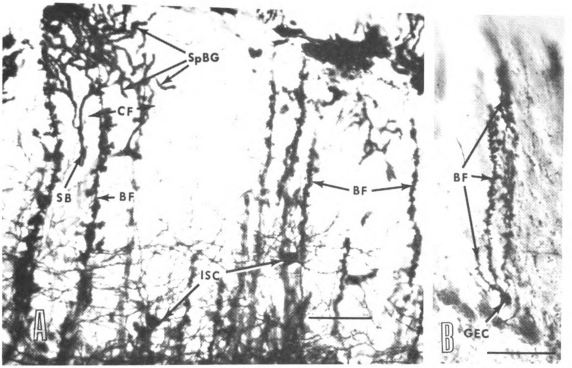


Figure 31. Lower power photomicrograph of the molecular layer. Abbreviations: BF = Bergmann fibers, CF = climbing fibers, GEC = Golgi epithelial cell, ISC = inferior stellate cell, SB = smooth branches, SpBG = spiny branchlets with gemmules. Rapid Golgi. Scale = 50 micra.

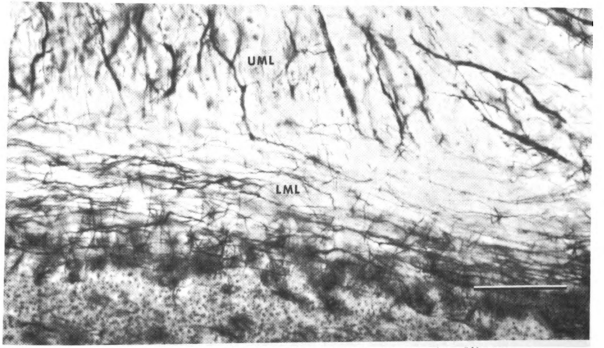
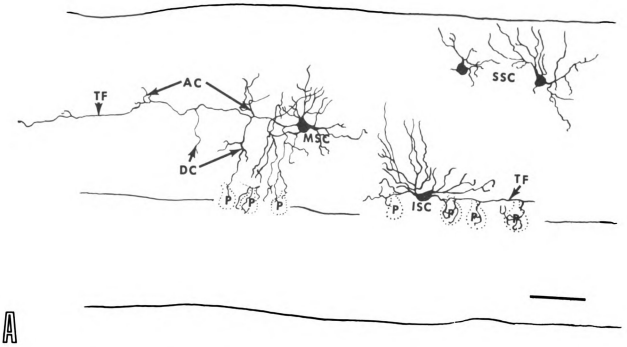
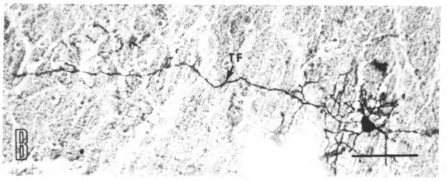


Figure 32. Photomicrograph showing the appearance of the fibers in the upper and lower portions of the molecular layer. Abbreviations: LML = lower part of molecular layer, UML = upper part of molecular layer. Golgi method VI. Scale = 50 micra.





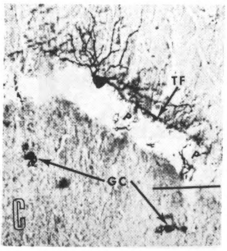


Figure 33. Tracings (A) and photomicrographs (B and C) of superior, middle and inferior stellate cells. Abbreviations: AC = ascending collateral, DC = descending collateral, GC = granular cell, ISC = inferior stellate cell, MSC = middle stellate cell, P = Purkinje cell, SSC = superior stellate cell, TF = transversal fiber. Figures 33-B and C are the same cells drawn in 33-A. Some of the processes are naturally out of the plane of focus. Rapid Golgi. Scale = 50 micra.

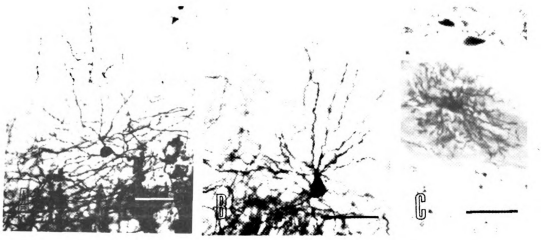


Figure 34. Photomicrographs of three typical stellate cells. Rapid Golgi. Scale = 50 micra.

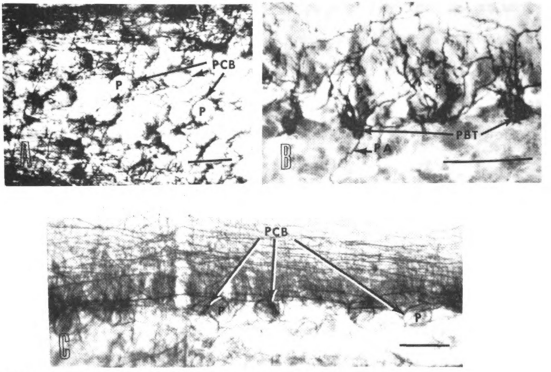


Figure 35. Photomicrographs of the pericellular arborizations and paint brush tip around the Purkinje cell. Abbreviations: PA = Purkinje axon, PBT = paint brush tip, PCB = Purkinje cell basket, P = Purkinje cell. Cajal method III, IV, Rapid Golgi. Scale = 35 micra.

CEREBELLAR NUCLEI

GENERAL INTRODUCTORY REMARKS

Cerebellar nuclei appear early in phylogeny as non-descript groups of multipolar neurons. A single unilateral cerebellar nucleus is first noticed in the lamprey (as the nucleus oclavomotorius), elasmobranchs (as the nucleus lateralis cerebelli or nucleus lateralis), and other lower vertebrate forms up to the reptiles (Larsell and Jansen, 1967). Beginning with the reptiles the cerebellar nuclear grey is divided into distinct medial and lateral nuclei (Nieuwenhuys, 1967). In the aves the cerebellar nuclei have been referred to as two, three, four or five (unilateral) cell masses (Larsell and Jansen, 1967). The general consensus of opinion is that in this particular vertebrate the cerebellar nuclei form a single undulating ribbon of cells with separate terminology applied to specific regions of the cellular ribbon (Ariens Kappers *et al.*, 1936; Doty, 1946).

In the Monotremata there are two cerebellar nuclei, simply described as medial and lateral (Hines, 1929; Abbie, 1934). Hines (1929) was of the opinion that the lateral nucleus corresponds to the dentate nucleus of higher mammals, while Abbie (1934) postulated that the lateral nucleus corresponds to the dentate and globosus nuclei of higher mammals. The latter felt that the medial cerebellar nucleus of the monotremata possibly represents the nuclei emboliformis and fastigii. Dillon (1962) did not discuss cerebellar nuclei.

In a study of the bat *(Myotis)* Larsell (1936a) stated that the bat has three cerebellar nuclei, a fastigii nucleus, interpositus

(or intermedius), and dentate nucleus. The interpositus nucleus is partially divided by bundles of fibers, giving the impression of a tentative division into emboliform and globosus nuclear regions.

In studies on the opossum, representing marsupials, Voris and Hoerr (1932) and Larsell (1935-36) reported that the cerebellar nuclear grey in this animal is divided into a dentate nucleus, interpositus nucleus, and medial nucleus. Voris and Hoerr considered the interpositus nucleus to be a "...medial and ventral prolongation of the nucleus dantatus...". Larsell did not agree with this and further stated:

> "The nucleus interpositus shows an incipient division by fibers into two parts, the globosus and emboliform nuclei of higher mammals."

Obenchain (1925), however, in a study of two South American marsupials, detected only two separate nuclear masses on each side of the cerebellum.

There are three cerebellar nuclei (unilaterally) in the rabbit, cat, and dog (Snider, 1940; Flood and Jansen, 1961; Singer, 1962). Based on the morphology of cell groups, Snider divided the nucleus interpositus of the rabbit into posterior and anterior regions. In the cat (Snider, and Flood and Jansen) the fastigii nucleus has been divided into a main fastigii nucleus and a subnucleus medialis parvocellularis; the interpositus nucleus into anterior and posterior regions; and the lateral nucleus into a main region and a subnucleus lateralis parvocellularis. The nucleus interpositus anterior is possibly homologues with the emboliform nucleus of man (Flood and

Jansen, 1961). These animals essentially have four nuclei unilaterally, the interpositus is merely in completely differentiated into two regions and the homologue of these regions are not yet definite.

In the higher primates and man there are four cerebellar nuclei unilaterally (Ariens Kappers *et al.*, 1936; Crosby *et al.*, 1962). Cooper and Courville (1968) have described the cerebellar nuclei of the *Macaca mullata*, and homologized them with the cerebellar nuclei in the cat. The cerebellar nuclei reach their highest point of differentiation in man comprising four separate (unilaterally) cellular masses. These are the fastigii nucleus, globosus nucleus, emboliformis nucleus, and the highly convoluted dentate nucleus from medial to lateral (Crosby *et al.*, 1962).

The author has been unable to find any literature on the cerebellar nuclei of any prosimian primate. Further consultation was carried out with Dr. Edward Lauer, University of Michigan, in an effort to locate any literature. Dr. Lauer informed the author that he could not find and was not aware of any studies on the cerebellar nuclei of the prosimians. In view of this void in the literature no comparisons or extrapolations can be drawn within the prosimians as a group, implications can only be inferred from higher and lower forms.

Larsell (1936a) has pointed out that it is possibly inadvisable to use the term lateral nucleus in lieu of dentate nucleus, since in submammalian forms the former gives rise, phylogenetically, to the mammalian dentate and interpositus nuclei. Due to the wide acceptance of the terms lateral (cerebellar) nucleus, and medial (cerebellar)

nucleus they will be used in the present study as synonymous with the terms dentate nucleus and fastigii nucleus respectively. The term interpositus nucleus will be retained since homologue of the emboliforms and flobosus nuclei in the prosimians cannot be established at this time. The complete lack of previous literature on prosimian cerebellar nuclei allows no comparison within the group, and it is not considered valid to extrapolate from higher forms with no intermediate stages. The establishment of homologues for the nucleus interpositus of the prosimian cerebellum must await studies on the cerebellar nuclei of a wide range of animals within the group as a whole.

GALAGO SENEGALENSIS[1]

The cerebellar nuclear grey matter of the lesser bushbaby is divisible into three distinct regions, a medial nucleus (fastigii or tectal), an interpositus nucleus, and a lateral nucleus (dentate) (Fig. 36, 37, 38). The lateral nucleus and interpositus nucleus are incompletely separated from each other, whereas the medial nucleus is entirely separate, throughout its entire extent, from the interpositus nucleus (Fig. 37).

The medial cerebellar nucleus of the *Galago* is an oval-shaped mass of cells located dorsally and slightly lateral to the fourth ventricle (Fig. 36-E, 37, 38). The medial nucleus is about 1200 micra by 800 micra at its greatest diameter and approximately 1600 micra at its greatest length (Fig. 39). Throughout its length the nucleus is slightly flattened dorsoventrally. It is first observed, in frontal section, about 450 micra caudal to the appearance of the interpositus nucleus as a scattered group of cells intermixed with large bundles of

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1. Note on Method

The following is an explanation of the method employed in constructing the drawings of the cerebellar nuclei of both animals of the present study.

The brains that were prepared specially for the drawings were serial sectioned and all sections mounted and stained. Tracings were made of 10 micra sections at intervals of either 100 or 200 micra. The interval between each drawing is indicated in each figure. Therefore two drawings would equal, for example, 120 micra; 10 micra for each of the two sections illustrated and 100 micra for the interval between the drawings. Using this method, height, width, and rostrocaudal depth were determined. For sake of clarity only the cerebellar nuclei are illustrated and the main portions of the cerebellar cortex are not illustrated. In each series of drawings A is the most rostral and N most caudal.

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fibers associated with the superior vestibular nucleus (Fig. 36-D). About 100 micra caudal to this point a distinct outline of the nucleus is clearly noted (Fig. 36-E). The nucleus rapidly enlarges in diameter (Fig. 37), then gradually tapers to a blunted caudal termination (Fig. 39). Rostral to a distinct medial nucleus (Fig. 36-A to C) there are large multipolar neurons intermixed with the fascicles from the superior vestibular nucleus. Because of the random arrangement of these cells there is not a sharp demarcation between the vestivular nucleus and the fastigii nucleus at this point, and cell bodies of the one appear to intermix with cell bodies of the other. This close association of vestibular and cerebellar nuclei in certain lower forms led Van Hoevell (1916) and Ariens Kappers (1921) to the conclusion that in the course of phylogeny the cerebellar nuclei had their origin from the vestibular nuclei. Recent studies suggest that the cerebellar nuclei have their greatest embryologic origin from within the cerebellum inself (Nieuwenhuys, 1967). In the caudal one-third of the medial nucleus (Fig. 37-J, 38) a small bundle of fibers appears to divide the nucleus into upper and lower portions. However no significant differences in cell size is observed below this bundle, therefore this region is not interpreted as a subnucleus. Flood and Jansen (1961) in a study on the cat described a subnucleus medialis parvicellularis in the ventral mid-one-third of the medial nucleus. Cooper and Courville (1968) did not mention this group of cells in the rhesus monkey *(Macaca mulatta)*. The cell bodies of the neurons of the medial cerebellar nucleus of the *Galago* are of two main types, a small fusi-

form cell body (14-18 micra) and medium-sized (20-26 micra) typical multipolar neurons (Fig. 40). Occasionally there appears to be a tendency for the smaller neurons to be found mainly in the ventral portion of the medial nucleus. Even when this appears to be the case larger neurons are freely intermixed with the smaller cells, therefore the small cells apparently do not form a subnucleus in the *Galago*.

The interpositus nucleus and the lateral cerebellar nucleus are incompletely separated from each other by relatively consistent fascicles of fine fibers (Fig. 37, 38). The lateral and interpositus nuclei are joined to varying degrees in the cat and rabbit (Snider, 1940; Flood and Jansen, 1961) and in the opossum (Voris and Hoerr, 1932; Larsell, 1935-36).

The fiber lamina separating the interpositus and lateral nuclei is consistently noticed throughout the rostro-caudal extent of these nuclei (Fig. 37, 38, 39). Due to the consistency of this lamina, the group of cell bodies medial to it is interpreted as the interpositus nucleus, and the group of cell bodies lateral to it is indicated as the lateral cerebellar nucleus (Fig. 37). The interpositus nucleus is about 1500 micra by 1000 micra at its greatest diameter and approximately 2100 micra at its greatest rostro-caudal extent. This nucleus therefore, extends furthest rostrad and caudad of any of the cerebellar nuclei in *Galago*. This nucleus is also slightly concave mediad toward the fastigii nucleus (Fig. 39). The large bundles of fibers that extend between the nucleus interpositus and fastigii nucleus are primarily responsible for the irregularities in the lateral side of

the fastigii nucleus (Fig. 39), but rarely cause irregularities in the medial side of the interpositus nucleus (Fig. 37, 39). Anterior and posterior portions of the interpositus nucleus have been described for the cat (Flood and Jansen, 1961) and the rhesus monkey (Cooper and Courville, 1968). In the *Galago* the nucleus interpositus appears to consist of a single cell mass. No anterior or posterior divisions could be determined either by differences in cell size, or by the orientation of fascicles of fibers. The nucleus interpositus is composed of multipolar cell bodies that are medium size to large (20-28 micra) (Fig. 41). Occasionally cell bodies as large as 30 micra are observed. Intermixed among the larger cells is a random population of small fusiform-like neurons that range from 14-18 micra (Fig. 41). There appears to be no regional localization for these smaller cells therefore they do not constitute a discrete subnucleus. It is entirely possible that these two ranges of cell size represent different functions, or different functional states.

The lateral cerebellar nucleus, or dentate nucleus, is the most lateral mass of nuclear grey in the *Galago* cerebellum. This lateral cell mass is interpreted as the lateral cerebellar nucleus for the following three reasons. [1] Even though it is only partially separated from the interpositus nucleus, the fibers that afford this separation extend throughout the rostro-caudal extent of this region. [2] The entire cell mass is notched in its lateral side (Fig. 37, 38), and has blunt dorsal and ventral extensions of cell bodies both on its rostral and caudal aspect. These corrugations are a suggestion of a primitive

beginning of the lamination of this cell mass so characteristic in higher primates. [3] The fiber lamina separating the lateral and interpositus nuclei, and the fibers entering the lateral nucleus from this region, suggest this area to be a primitive hilus, a condition similar to that seen in the cat (Flood and Jansen, 1961). These points are illustrated in figures 37, 38, and 39. Despite the apparent beginnings of laminations in the lateral nucleus it has the shortest rostral caudal extent (Fig. 39), only about 1550 micra, or any of the cerebellar nuclei. In frontal section the lateral nucleus is slightly pyramidal in shape, the base facing laterally and the apex flattened against the fiber lamina separating the lateral and interpositus nuclei (Fig. 37, 38). This gives the lateral nucleus an approximate diameter of 1300 micra by 1200 micra at its greatest point. A subnucleus of the lateral cerebellar nucleus has been described in the rabbit and cat by Snider (1940), and tentatively named subnucleus lateralis parvicellularis in the cat by Flood and Jansen (1961). In the *Galago* the cell bodies of the neurons of the lateral nucleus range from 20 - 28 micra with an intermixed population of smaller cells (14 - 18 micra) (Fig. 42). The smaller cells are not organized into any specific discrete groups therefore the lateral nucleus of the *Galago* cerebellum does not appear to have any subdivisions. Larsell (1935-36), in a study of the opossum, applied the term pars paraflocculari s to that portion of the lateral nucleus that extends laterally and ventrally toward the paraflocculus. This extension of cells is pronounced in the *Galago* (Fig. 37-D). Ariens

Kappers (1921) termed this extension of cell bodies the pars flocularis, and Jansen (1933) preferred the noncommittal term pars lateralis. Since it is not known whether this lateral extension of the lateral nucleus is functionally associated with the paraflocculus perhaps the term pars lateralis should be tentatively accepted (Jansen, 1933).

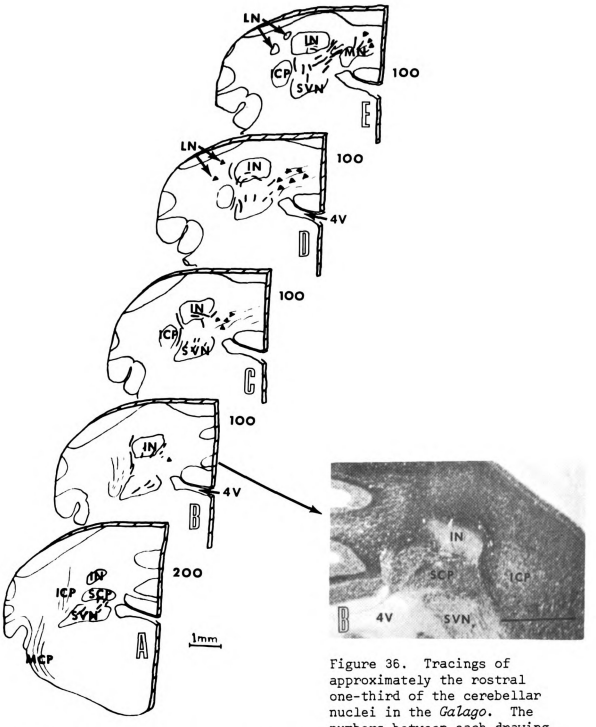

Figure 36. Tracings of approximately the rostral one-third of the cerebellar nuclei in the *Galago*. The numbers between each drawing represent the depth, in micra, separating each drawing. The triangles represent the location of cell bodies and are not drawn to scale. Abbreviations: ICP = inferior cerebellar peduncle, IN = interpositus nucleus, LN = lateral nucleus, MCP = middle cerebellar peduncle, MN = medial nucleus, PL = pars lateralis, SCP = superior cerebellar peduncle, SVN = superior vestibular nucleus, 4V = fourth ventricle. Luxol fast blue-cresylecht violet. The photomicrograph is a mirror image of its corresponding drawing. Photomicrograph scale = 1 mm.

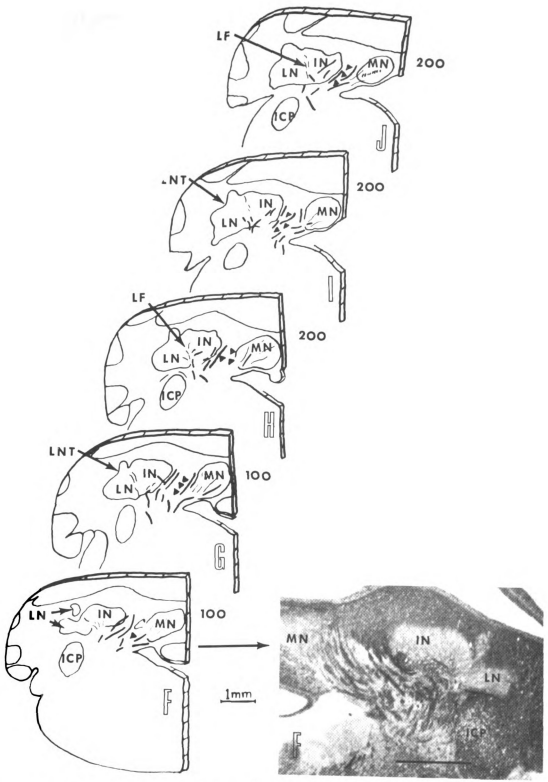

Figure 37. Tracings of approximately the middle third of the cerebellar nuclei in the *Galago*. Abbreviations: LF = lamina of fibers, LNT = lateral notch in the lateral nucleus. For additional abbreviations see Figure 36. Luxol fast blue-cresylecht violet. The photomicrograph is a mirror image of its corresponding drawing. Photomicrograph scale = 1 mm.

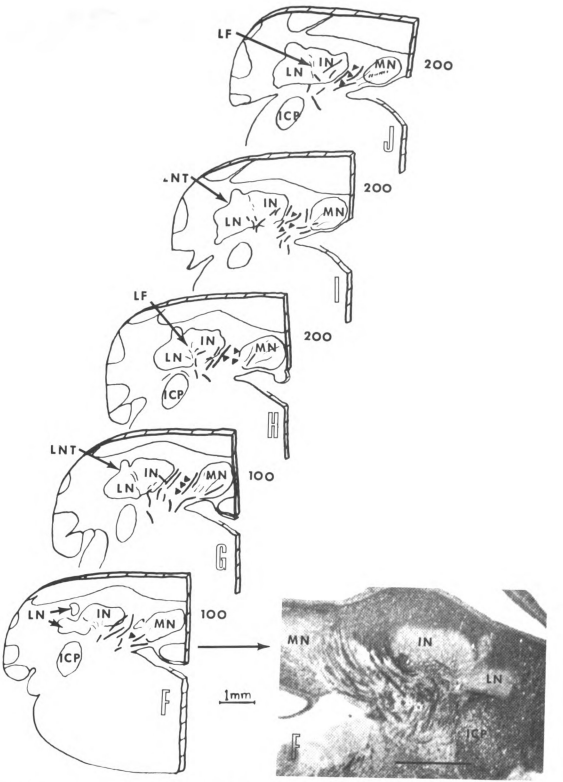

Figure 37. Tracings of approximately the middle third of the cerebellar nuclei in the *Galago*. Abbreviations: LF = lamina of fibers, LNT = lateral notch in the lateral nucleus. For additional abbreviations see Figure 36. Luxol fast blue-cresylecht violet. The photomicrograph is a mirror image of its corresponding drawing. Photomicrograph scale = 1 mm.

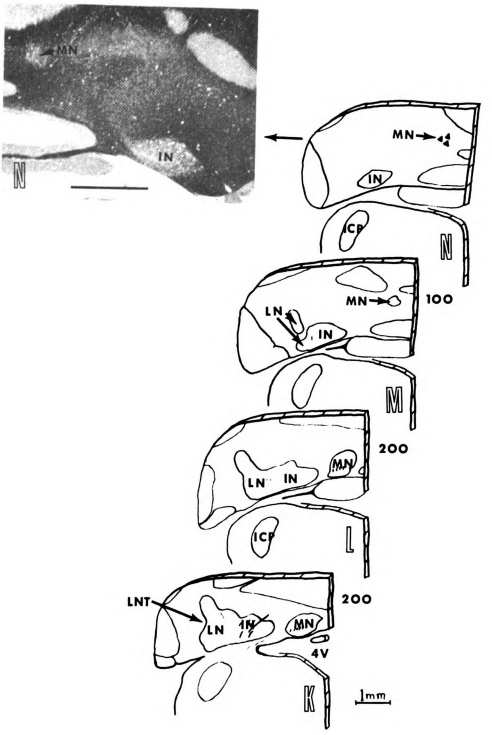

Figure 38. Tracings of about the caudal third of the cerebellar nuclei in the *Galago*. For abbreviations see Figures 36, 37. Luxol fast blue-cresylecht violet. The photomicrograph is a mirror image of its corresponding drawing. Photomicrograph scale = 1 mm.

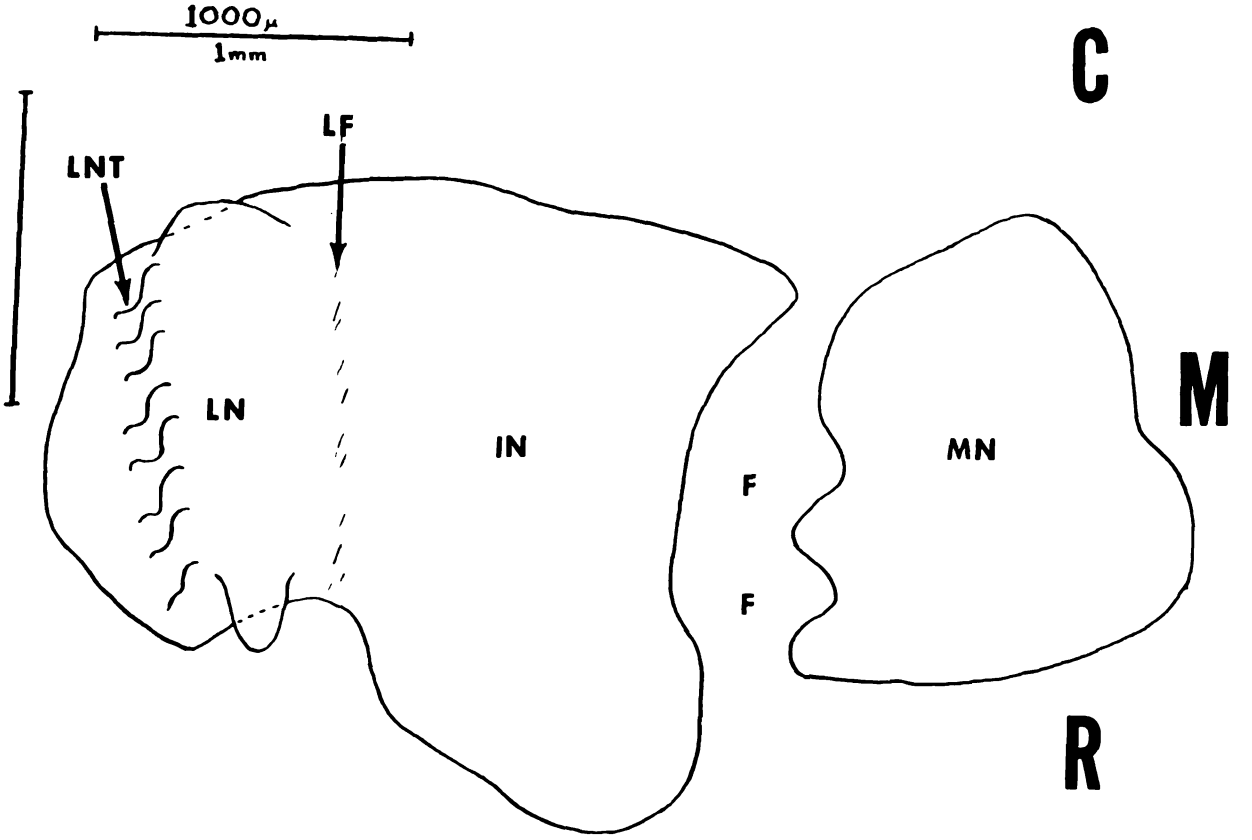

Figure 39. A diagrammatic dorsal view of the cerebellar nuclei of the *Galago* drawn to scale. Abbreviations: C = caudal, F = position of fiber bundles, IN = interpositus nucleus, LF = lamina of fibers, LN = lateral nucleus, LNT = lateral notch in lateral nucleus, M = medial, MN = medial nucleus, R = rostral.

Figure 40. Photomicrograph and tracings of multipolar cell bodies of the medial cerebellar nucleus. Cell bodies are outlined by arrows. (A) Luxol fast blue-cresylecht violet, (B) Cajal method VI. Scale = 50 micra. (B in figures 40, 41, 42 are traced from cells stained in silver. Photomicrographs of this stain appear in figures 47, 48, 49.)

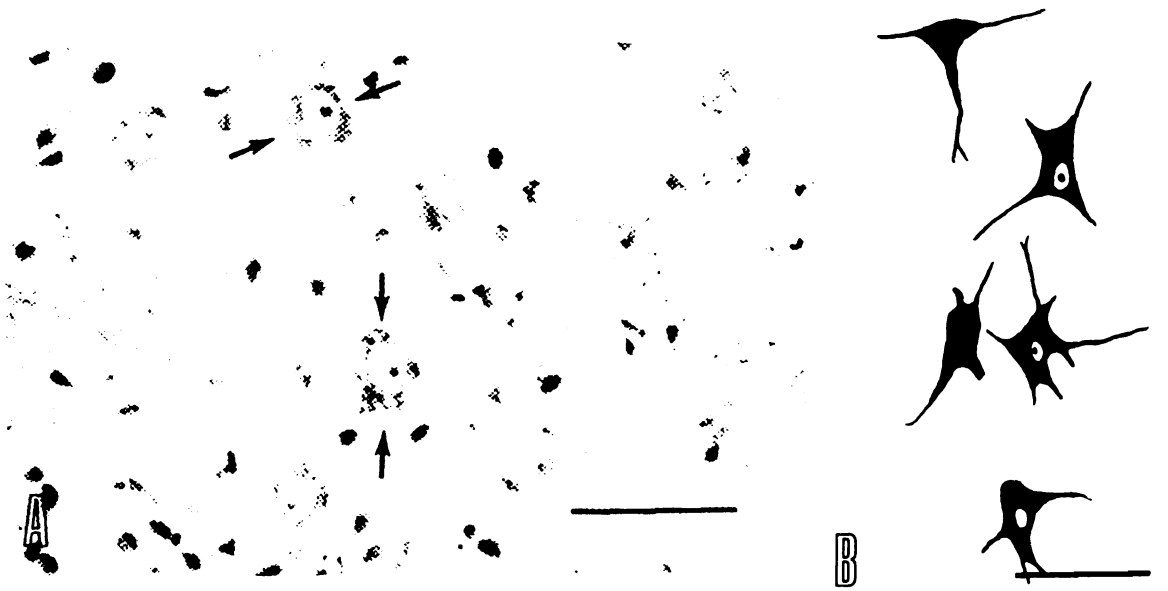

Figure 41. Photomicrograph and tracings of multipolar cell bodies of the interpositus nucleus. Cell bodies are outlined by arrows. (A) Luxol fast blue-cresylecht violet, (B) Cajal method VI. Scale = 50 micra.

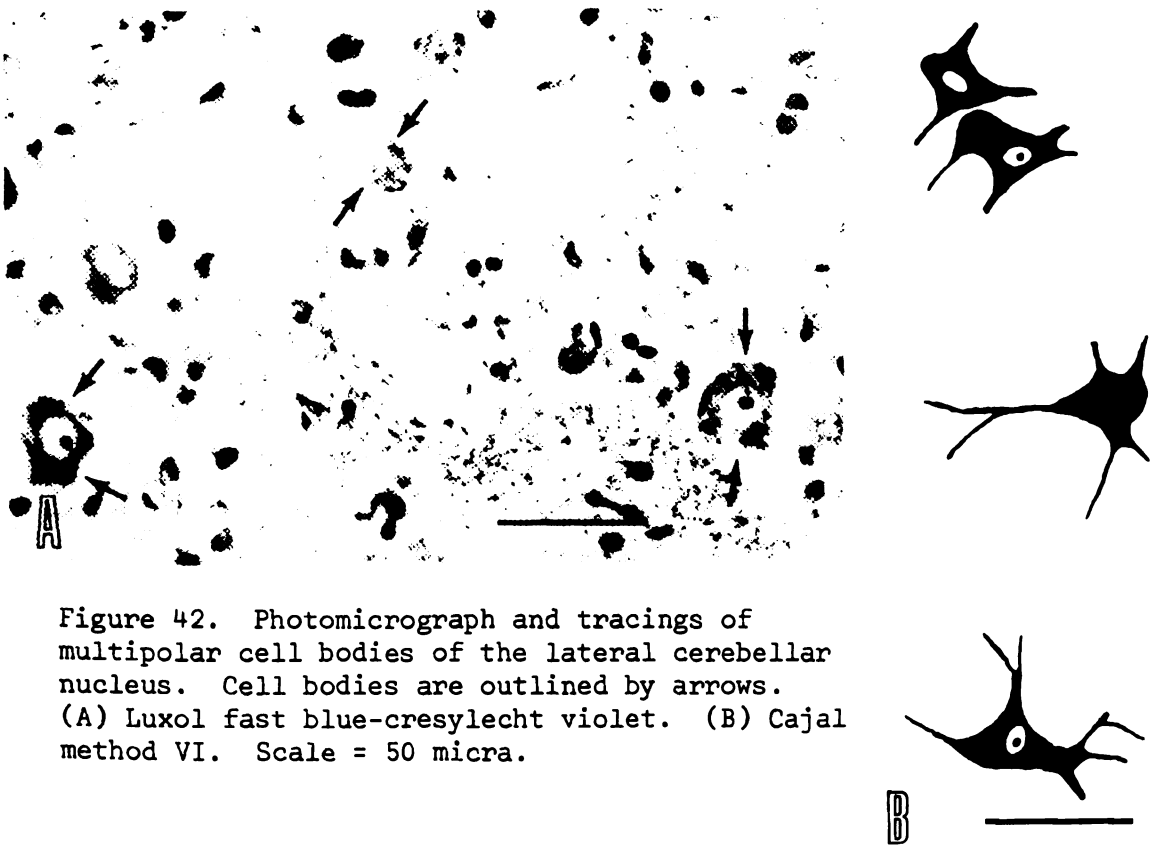

Figure 42. Photomicrograph and tracings of multipolar cell bodies of the lateral cerebellar nucleus. Cell bodies are outlined by arrows. (A) Luxol fast blue-cresylecht violet. (B) Cajal method VI. Scale = 50 micra.

TUPAIA GLIS

The cerebellar nuclear grey matter of the tree shrew is made up of three regions, a distinct medial cerebellar nucleus (fastigii or tectal), and a nucleus interpositus that is incompletely separated from the lateral nucleus (dentate) (Fig. 42, 43, 44). Throughout most of their rostro-caudal extent the interpositus and lateral nuclei are partially separated from each other by an irregular lamina of thin fibers (Fig. 43). The medial cerebellar nucleus is always completely separated from the interpositus nucleus by thick bundles of fibers that appear to issue, in part, from the superior vestibular nucleus (Fig. 42, 45).

The medial nucleus of the cerebellum of *Tupaia* is an oval-shaped mass of cells with a laterally directed, and slightly tapered, caudal half (Fig. 45). From rostral to caudal the medial nucleus is located dorsal to the fourth ventricle. It is about 1350 micra by 1000 micra at its greatest diameter and approximately 1100 micra long in its greatest rostro-caudal length. The medial nucleus first appears as scattered cells amid coarse bundles of fibers about 500 micra caudal to the appearance of the interpositus and lateral nuclei on frontal section (Fig. 44-F). Within a distance of 100-150 micra caudad of these scattered cells, a distinct outline of the medial cerebellar nucleus is observed. In the large bundles of fibers that separate the interpositus and medial nuclei there are scattered cell bodies, therefore there is not a sharp border between the superior vestibular nucleus and the medial cerebellar nucleus particularly in the rostral

area of the latter. A small group of cells appears within the large fiber bundles (Fig. 44-G) but eventually it coalesces with the fastigii nucleus, and is interpreted as a laterally detached portion of the medial nucleus. The cell bodies of the neurons in the medial nucleus range from 18-30 micra. The smaller cell bodies (18-24 micra) seem to have finer Nissl bodies while the larger cell bodies (25-30 micra) appear to have larger Nissl bodies (Fig. 46). These two cell body sizes are intermixed and no subnucleus could be determined. A subnucleus medialis parvicellularis of the medial cerebellar nucleus has been identified and described in the cat and rabbit (Snider, 1940; Flood and Jansen, 1961).

The interpositus nucleus and the lateral cerebellar nucleus of the *Tupaia* are incompletely separated from each other throughout their rostro-caudal extent by an irregular lamina of fine fibers (Fig. 43, 44). An incomplete separation of these nuclei has been reported in a variety of mammalian forms (Voris and Hoerr, 1932; Ariens Kappers, *et al.*, 1936; Snider, 1940; Flood and Jansen, 1961; Singer, 1962).

The interpositus nucleus of the tree shrew is interpreted as that group of cells medial to the lamina of thin fibers, and it is the largest rostro-caudal group of cell bodies in the *Tupaia* cerebellum. It is approximately 1200 micra by 1000 micra at its greatest diameter and about 1700 micra at its greatest length (Fig. 45). It is essentially an elongated oval with slight variations in its medial boundary. This irregular medial border is apparently not a result of the coarse bundles of fibers that affect the configuration of the medial nucleus.

The interpositus nucleus has a deep concavity toward the medial nucleus (Fig. 45). Anterior and posterior nuclei of the interpositus have been described in a variety of animals (Ariens Kappers *et al.*, 1936; Snider, 1940; Flood and Jansen, 1961), with the greatest degree of differentiation of the interpositus region occurring in man (Crosby *et al.*, 1962). In the tree shrew it appears that there are no subnuclei of the interpositus, based either on cell size or on the positioning of fiber bundles in the nucleus. The cell bodies of the neurons of the interpositus nucleus are multipolar and range from 20 - 26 micra (Fig. 47).

The most lateral cell mass of the *Tupaia* cerebellum is partially separated from the interpositus nucleus and, based on the following three points, is interpreted as the dentate nucleus. [1] The lamina of fibers separating the lateral and interpositus nuclei is seen throughout the rostro-caudal extent of this region. [2] The lateral nucleus is slightly notched on its lateral side suggesting the very beginnings of a lamination of this nucleus, a condition highly developed in high primates and man. The notches in the *Tupaia* lateral cerebellar nucleus are not as pronounced as they are in the *Galago*. The fiber lamina separating the lateral and interpositus nuclei and the fibers entering the lateral nucleus from this lamina give the impression of a primitive hilus of the dentate nucleus (Fig. 43). A situation similar to this is seen in the cat (Flood and Jansen, 1961). The lateral cerebellar nucleus is an oval-shaped mass of cells approximately 1500 micra by 1500 micra at its greatest diameter

but only about 1450 micra at its greatest length (Fig. 45). In serial frontal sections the lateral nucleus appears at about the same level, or slightly caudal to, the appearance of the interpositus nucleus. Within a distance of 300 micra these two nuclei join dorsally and remain partially connected throughout most of their rostrocaudal extent. A subnucleus of the lateral cerebellar nucleus in the cat was proposed by Snider (1940), and tentatively confirmed by Flood and Jansen (1961). In the tree shrew no subdivision of the lateral nucleus is noted. The cell bodies of the neurons of the lateral nucleus are multipolar and range from 20 - 30 micra (Fig. 48). The smaller neurons appear to be more fusiform in shape then the larger neurons, however they do not appear to form a parvicellular region. The ventral and lateral projection of cell bodies from the lateral nucleus has been termed the pars floccularis (Ariens Kappers, 1921), the pars lateralis (Jansen, 1933), and the pars paraflocculari s (Larsell 1935-36). In the *Tupaia* this extension of cell bodies is not pronounced, and the term pars lateralis is adopted from Jansen (1933) for the present study.

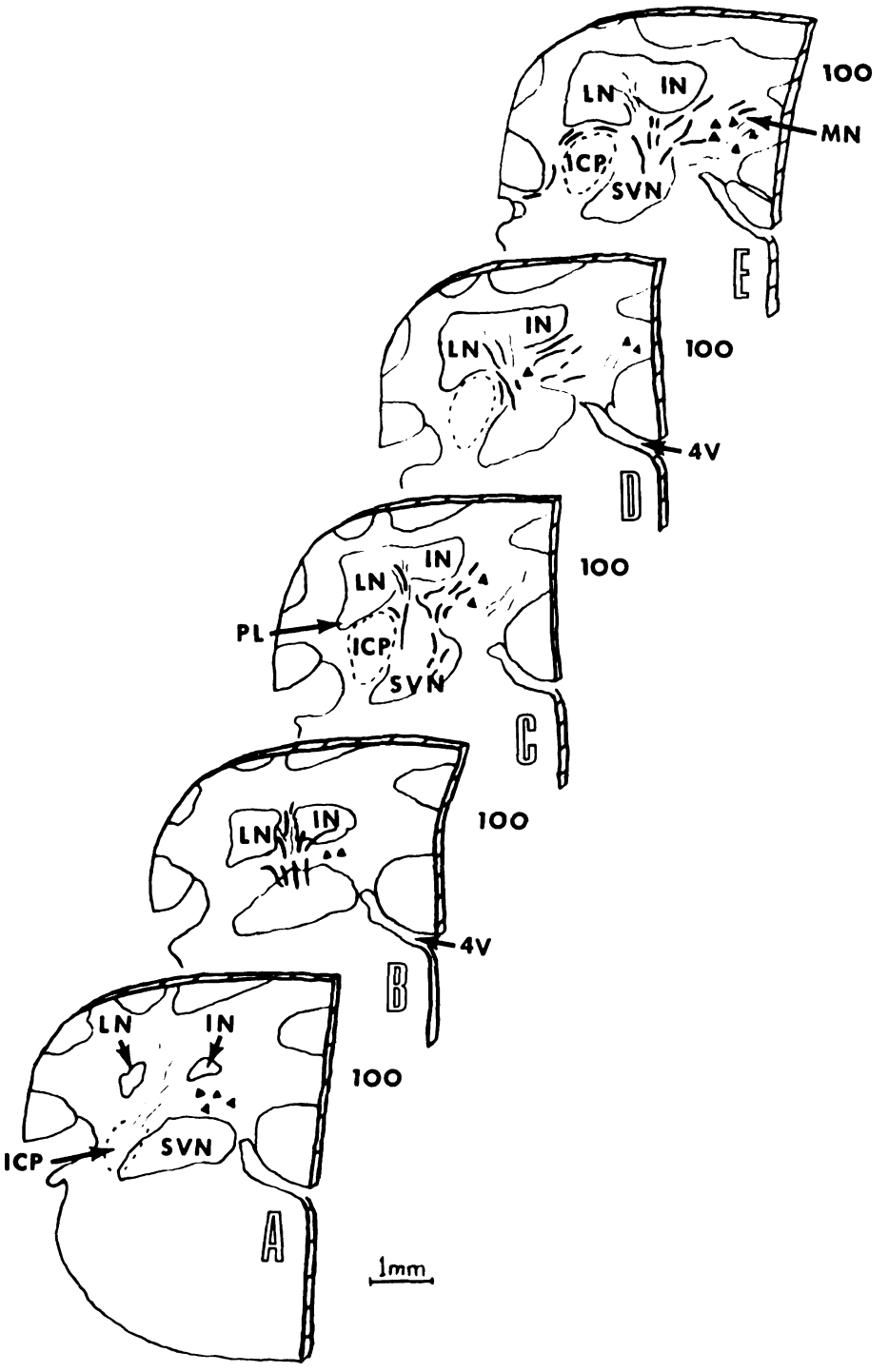

Figure 43. Tracings of about the rostral third of the cerebellar nuclei in the *Tupaia*. The numbers between each drawing represent the micra separating each drawing. The triangles represent the locations of cell bodies, and are not drawn to scale. Abbreviations: ICP = inferior cerebellar peduncle, IN = interpositus nucleus, LF = lamina of fibers, LN = lateral nucleus, MN = medial nucleus, PL = pars lateralis, SVN = superior vestibular nucleus, 4V = fourth ventricle.

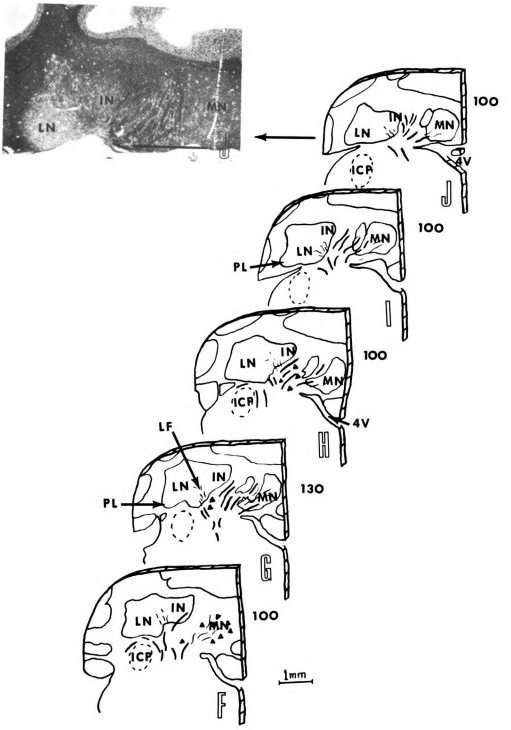

Figure 44. Tracings of about the middle third of the cerebellar nuclei in *Tupaia*. Abbreviations: LNT = lateral notch in lateral nucleus. For additional abbreviations see Figure 43. Luxol fast blue-cresylecht violet. Photomicrograph scale = 1 mm.

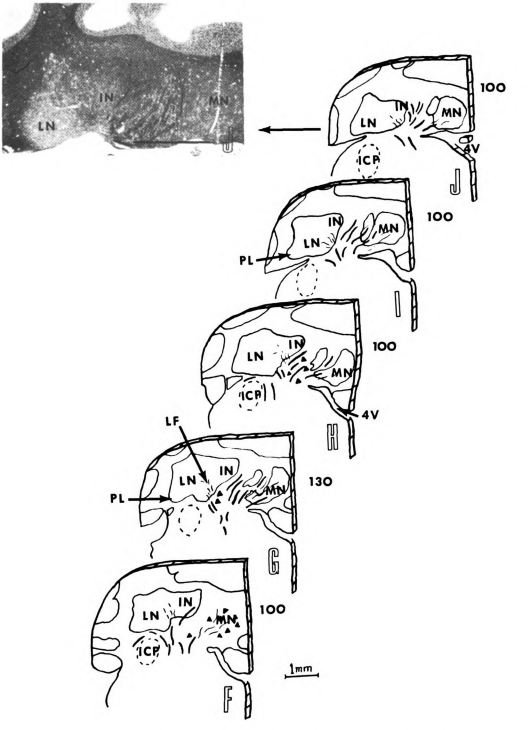

Figure 44. Tracings of about the middle third of the cerebellar nuclei in *Tupaia*. Abbreviations: LNT = lateral notch in lateral nucleus. For additional abbreviations see Figure 43. Luxol fast blue-cresylecht violet. Photomicrograph scale = 1 mm.

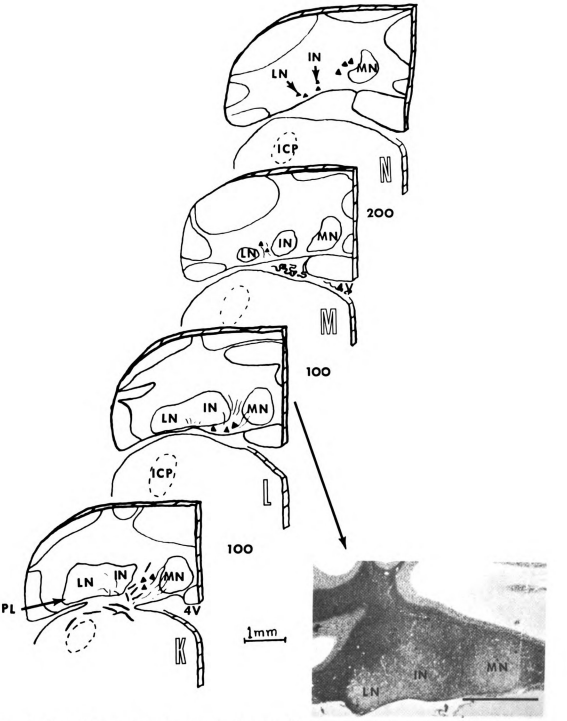

Figure 45. Tracings of about the caudal third of the cerebellar nuclei in *Tupaia*. For abbreviations see Figures 43, 44. Luxol fast blue-cresylecht violet. Photomicrograph scale = 1 mm.

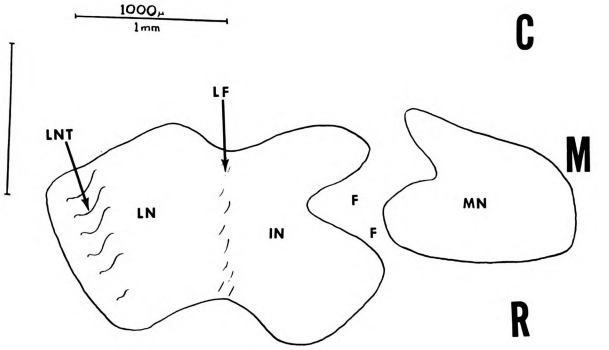

Figure 46. A diagrammatic dorsal view of the cerebellar nuclei of *Tupaia*. Abbreviations: C = caudal, F = position of fiber bundles, IN = interpositus nucleus, LF = lamina of fibers, LN = lateral nucleus, LNT = lateral notch in lateral nucleus, M = medial, MN = medial nucleus, R = rostral.

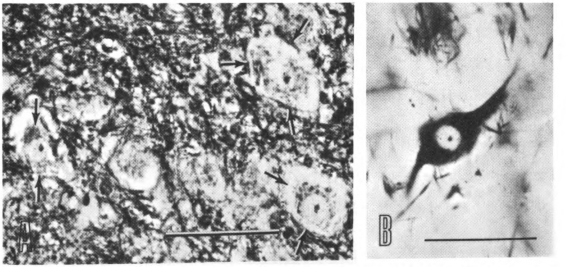

Figure 47. Photomicrographs of the multipolar cell bodies of the medial cerebellar nucleus. Cell bodies are outlined by arrows. (A) Luxol fast blue-cresylecht violet, (B) Cajal method VI. Scale = 50 micra.

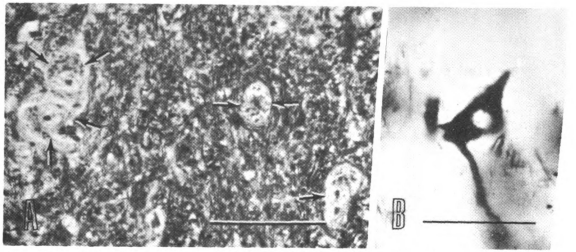

Figure 48. Photomicrographs of the multipolar cell bodies of the neurons of the interpositus nucleus. Cell bodies are outlined by arrows. (A) Luxol fast blue-cresylecht violet, (B) Cajal method VI. Scale = 50 micra.

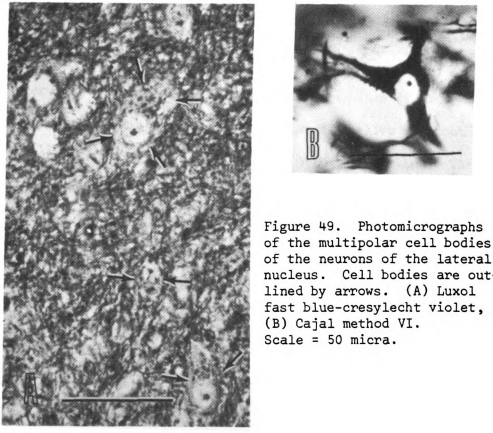

Figure 49. Photomicrographs of the multipolar cell bodies of the neurons of the lateral nucleus. Cell bodies are outlined by arrows. (A) Luxol fast blue-cresylecht violet, (B) Cajal method VI. Scale = 50 micra.

CORRELATIVE DISCUSSION

The *Galago* and *Tupaia* each have three nuclei in each half of their cerebellum, a medial nucleus, interpositus nucleus, and a lateral nucleus. In both animals the medial nucleus is located dorsal to the fourth ventricle and separated from the interpositus by coarse bundles of fibers. The interpositus and lateral nuclei are partially joined throughout their rostro-caudal extent. The cell bodies of the neurons making up the cerebellar nuclei of *Galago* and *Tupaia* are multipolar and range from 18 - 30 micra in both animals. The smaller cell bodies (18 - 25 micra) appeared to be fusiform in shape, but in silver sections these were still observed to be multipolar neurons.

In an overall comparison the cerebellar nuclei of the *Galago* are slightly larger than the nuclei of *Tupaia* (Fig. 50). This is probably in part related to the fact that the *Galago* cerebellum is about one-fifth larger in its overall size than the *Tupaia* cerebellum. The medial nucleus in both animals is composed of multipolar cell bodies and separated from the nucleus interpositus. In the busybaby the entire nucleus is a slightly elongated oval, while in the tree shrew the caudal half is tapered to a medially projecting blunt end.

Those heavy bundles of fibers separating the medial and interpositus nuclei are characterized in both animals by having multipolar cell bodies interspersed among them. In the avian cerebellum cell bodies located in bundles of fibers have been interpreted as bridges of cells connecting various portions of the cerebellar nuclei (Doty, 1946).

The cell bodies located in the coarse fiber bundles are continuous with cell bodies of the superior vestibular nucleus. At this time these cells are interpreted as merely a random population of cells and are not suggested as a specific nucleus. In frontal sections, once the fastigii nucleus is reached its limits can be clearly determined (Fig. 44). In relation to this extension of superior vestibular cells upward into the substance of the cerebellum Van Hoevell (1916) and Ariens Kappers (1921) postulated that the deep cerebellar nuclei have their origin from the vestibular complex. These authors felt that in the process of phylogeny cell bodies of the vestibular complex became progressively more segregated upward to assume an intracerebellar position in higher forms. Larsell (1947) and Rudeberg in 1961 (Nieuwenhuys, 1967) were of the opinion that most of the cerebellar nuclei have their origin from within the cerebellum itself.

The most obvious difference between the cerebellar nuclei of the *Galago* and *Tupaia* is the macroscopic appearance and extent of the lateral cerebellar nucleus. In the *Tupaia* the only hint of attempts at lamination is a slight notch on the lateral side of the nucleus (Fig. 44). In the *Galago* the lateral notch is greatly pronounced (Fig. 37), and the lateral nucleus has dorsal and ventral extensions of cells from its rostral and caudal aspects (Fig. 50). This gives the impression, when compared to *Tupaia*, of a progressive development of the dentate nucleus toward the more highly laminated structure seen in higher primates and man (Ariens Kappers, *et al.*, 1936). The pars parafloccularis of Larsell (1935-36) and pars lateralis of Jansen (1933) is more pronounced in the *Galago* than it is in the *Tupaia*.

The cerebellar nuclei of both prosimians in the present study are obviously of primitive form, the *Tupaia* only slightly more so than the *Galago*. For several reasons no suggestion on the phylogeny of the tree shrew is made based on the cerebellar nuclei. Principle of these is the lack of information on other prosimian forms, and on insectivores. Many studies on key phylogenetic animals, excellent as they may be, deal only with the gross anatomy of the cerebellum and do not include the nuclei (e.g. Dillon, 1962; 1963). Phylogenetic implications of the cerebellar nuclei of the prosimians of this study, and other prosimians in general, await broader investigations within this group of animals.

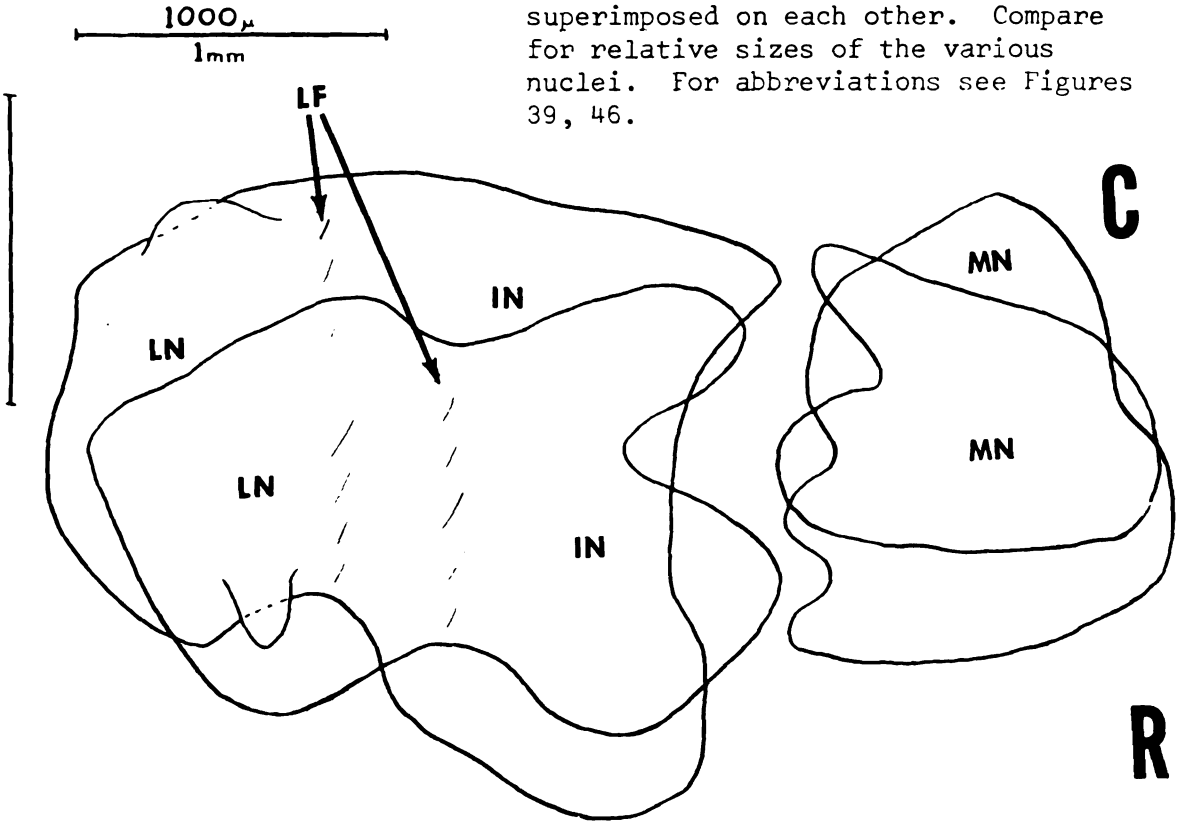

Figure 50. A diagrammatic dorsal view of the cerebellar nuclei of *Galago* and *Tupaia* drawn on the same scale, and superimposed on each other. Compare for relative sizes of the various nuclei. For abbreviations see Figures 39, 46.

SUMMARY AND CONCLUSIONS

The cerebelli of two groups of prosimian primates have been studied grossly and microscopically. The lesser bushbaby *(Galago senegalensis)* represents a more advanced prosimian, whereas the tree shrew *(Tupaia glis)* represents the borderline prosimian-insectivore.

Grossly the cerebellum of the bushbaby is approximately one-fifth larger than the cerebellum of the tree shrew. In mid-sagittal section cerebelli of both animals had the same total number of consistent fissures, sulci, and sublobules.

The anterior lobe of the *Galago* has lateral extensions of the central lobule and culmen lobule designated as central lobe pars lateralis and culmen pars lateralis in this study. The tree shrews used in this study did not have hemispheric portions of these lobules, but had a well developed vermal central lobule and vermal culmen.

The middle and posterior lobes of the cerebellum show similar characteristics in each animal. The lobulus simplex is usually a single folium in both animals, although in some of the *Galago* it was subdivided by a shallow intrinsic sulcus. The declive region of the vermis is slightly larger in *Tupaia* and *Galago*, but the tuber is a single folium in both. The hemispheres of the prosimian cerebellum are lateral extensions of the middle lobe. The cerebellar hemisphere of *Galago* is made up of central lobe pars lateralis, culmen pars lateralis, crus I and II of the ansiform lobule and the paramedian lobule. In the tree shrew the ansiform lobule is greatly enlarged comprising 4 - 5 folia compared to 2 folia in the bushbaby. It is a known fact

that various brain stem nuclei, particularly the pontine nuclei, project to the ansiform lobule. Various fiber projections as well as the anatomy of the ansiform lobule of higher primates were discussed and it was suggested that the advanced development of the ansiform lobule in *Tupaia*, is more characteristic of primates than insectivores. The paramedian lobule is composed mainly of four folia in the *Galago* and *Tupaia*.

The pyramidal lobule in the tree shrew is consistently less well developed than the pyramidal lobule of *Galago*. The relationship of the pyramidal lobule and certain portions of the anterior lobe to forward and backward balance was discussed. It was concluded that the degree of development of these regions is partially related to the mode of locomotion.

The band of cortical grey that joins the paraflocculus to the pyramidal lobule is vertically fissured in the *Tupaia* and horizontally fissured in the *Galago*. When compared to a wide range of mammals it was concluded that fissures in the copula represent a progressive phylogenetic characteristic, and that this occurrence in *Tupaia* also suggest a closer affiliation to primates.

The flocculus and paraflocculus are larger and more differentiated in *Tupaia* than in the *Galago*. The paraflocculus serves in the reception of incoming proprioception and it is suggested that its advanced development in *Tupaia* possibly offsets the limited development of functionally related portions of the anterior lobe. The development of the flocculus is related to eye movement. The present study shows that

the more advanced development of the flocculus in *Tupaia* can be correlated with the wider range of eye movement in this animal over the *Galago*.

The cytoarchitecture of the cerebellar cortex was studied with standard Nissl stains, and various silver techniques. The histologic structure of the cortex in *Tupaia* and *Galago* is essentially similar to that of the rhesus monkey (Fox *et al.*, 1967).

The macroscopic appearance and cytoarchitecture of the cerebellar nuclei were also studied with Nissl stains and silver techniques. There are three cerebellar nuclei in both of the prosimians used in this study, a medial or fastigial nucleus, an interpositus nucleus, and a lateral or dentate nucleus. The medial nucleus is separated from the lateral nucleus by coarse bundles of fibers intermixed by neuron cell bodies. The interpositus and lateral nucleus are partially joined throughout their rostro-caudal extent. The lateral nucleus has a lateral notch in the *Tupaia*, which has been interpreted as the beginnings of a lamination of this nucleus. In the *Galago* this notch is accentuated, and the lateral nucleus has acquired additional extensions of cells from its rostral and caudal aspects. This was interpreted as a slight advancement in the lamination of the lateral nucleus. The lamina of thin fibers that partially separates the interpositus and lateral nuclei also appears to form the primitive hilus of the dentate nucleus in *Tupaia* and *Galago*.

LITERATURE CITED

Abbie, A. A. 1934. The brain-stem and cerebellum of *Echidna aculeata*. Philo. Trans. Roy. Soc. Lond. ser B. 224:1-74.

Ariens Kappers, C. U. 1921. *Die vergleichende Anatomie des Nervensystems der Wirbeltiere und des Menschen.* E. F. Bohn, Haarlem.

Ariens Kappers, C. U., G. C. Huber, E. C. Crosby. 1936. *The Comparative Anatomy of the Nervous System of Vertebrates Including Man.* Vol. I. MacMillan Co., New York pp. 696-833.

Bradley, O. C. 1904. The mammalian cerebellum: Its lobes and fissures. Part I. J. Anat. 38:448-475.

_____ 1904-05. The mammalian cerebellum: Its lobes and fissures. Part II. J. Anat. 39:99-117.

Braitenberg, B., and R. Atwood. 1958. Morphological observations on the cerebellar cortex. J. Comp. Neur. 109:1-34.

Brodal, A. 1940a. Modification of the Gudden method for study of cerebellar localization. Arch. Neurol. Psychiat. 43:46-58.

_____ 1940b. Experimentelle Untersuchungen uber die olivocerebellare Localisation. Z. ges. Neurol. Psychiat. 169:1-153.

_____ 1967. Anatomical studies of cerebellar fibre connections with special reference to problems of functional localization. In: *The Cerebellum. Vol. 25. Progress in Brain Research.* Elseiver, New York pp. 135-173.

Brodal, A. and B. Hoivik. 1964. Site and mode of termination of primary vestibulocerebellar fibres in the cat. An experimental study with silver impregnation methods. Arch. ital. Biol. 102:1-21.

Brodal, A. and J. Jansen. 1946. The ponto-cerebellar projections in the rabbit and cat. Experimental investigations. J. Comp. Neur. 84:31-118.

Buettner-Janusch, J. 1963. An introduction to the primates. In: Evolutionary and Genetic Biology of the Primates. Vol. I Academic Press, New York pp. 1-64.

_____ 1966. *Origins of Man.* John Wiley & Sons, Inc., New York pp. 13-16, 193-202.

Campbell, C. B. G. 1965. Pyramidal tracts in primate taxonomy. Ph.D. thesis, University of Ill., Chicago, Ill.

_____ 1966a. Taxonomic status of tree shrews. Sci. 153:436.

_____ 1966b. The relationships of the tree shrews: the evidence of the nervous system. Evolution 20:276-281.

Campbell, C. B. G., J. A. Jane, and D. Yashon. 1966. The retinal projections of tree shrew and hedgehog. Anat. Rec. 154:326.

Carpenter, M. B. and N. L. Strominger. 1965. The medial longitudinal fasciculus and disturbances of conjugate horizontal eye movements in the monkey. J. Comp. Neur. 125:41-66.

Carpenter, M. B. 1967. Central connections of the vestibular system. Arch. Otolaryying. 85:73-76.

Chang, H-T. and T. C. Ruch. 1949. The projection of the caudal segments of the spinal cord to the lingula in the spider monkey. J. Anat. 83:303-307.

Conn, J. J., M. A. Darrow, and V. M. Emmel. 1962. *Staining Procedures used by the Biological Stain Commission.* Williams and Wilkins Co., Baltimore.

Cooper, C. W. and J. Courville. 1968. The cerebellar nuclei of *Macaca mulatta.* A morphological study. Anat. Rec. 160:334-335.

Crosby, E., T. Humphrey, and E. Lauer. 1962. *Correlative Anatomy of the Nervous System.* MacMillan Co., New York pp. 188-192.

Detwiler, S. R. 1939. Comparative studies upon the eyes of nocturnal lemuroids, monkeys, and man. Anat. Rec. 74:129-145.

Dillon, L. S. 1962. Comparative notes on the cerebellum of the monotremes. I. Contribution toward a phylogeny of the mammalian brain. J. Comp. Neur. 118:343-353.

_____ 1963. Comparative studies of the brain in the Macropodidae. Contribution to the phylogeny of the mammalian brain II. J. Comp. Neur. 120:43-51.

Doty, E. J. 1946. The cerebellar nuclear gray in the sparrow *(Passer domesticus).* J. Comp. Neur. 84:17-30.

Dow, R. S. 1936. The fiber connections of the posterior parts of the cerebellum in the rat and cat. J. Comp. Neur. 63:527-548.

Eccles, J. C., M. Ito, and J. Szentagothai. 1967. *The Cerebellum as a Neuronal Machine.* Springer-Verlag, New York Inc., New York.

Einarson, L. 1932. A method for progressive selective staining of Nissl and nuclear substances in nerve cells. Amer. J. Path. 8:295-309.

Elliot Smith, G. 1899a. The brain in the edentata. Trans. Linn. Soc. ser. 2,7:277:394.

_____ 1899b. Further observations on the anatomy of the brain in the Monotremata. J. Anat. Physiol. 33:309-345.

_____ 1902a. The primary subdivisions of the mammalian cerebellum. J. Anat. 36:381-385.

_____ 1902b. Notes on the brain of *Macroscelides* and other Insectivora. Linn. Soc. J. Zool. 28:443-448.

_____ 1903a. On the morphology of the brain in the mammalia, with special reference to that of the lemurs recent and extinct. Trans. Linn. Soc. Long. ser. 2. 8:319-432.

_____ 1903b. Further observations on the natural mode of subdivision of the mammalian cerebellum. Anat. Anz. 23:368-384.

Flood, S. and J. Jansen. 1961. On the cerebellar nuclei in the cat. Acta Anat. 46:52-72.

Fox, C. A. 1959. The intermediate cells of Lugaro in the cerebellar cortex of the monkey. J. Comp. Neur. 112:39-53.

_____ 1962. The structure of the cerebellar cortex. In: *Correlative Anatomy of the Nervous System,* E. C. Crosby, T. H. Humphrey and E. W. Lauer. New York. The MacMillan Co. pp. 193-198.

Fox, C. A., D. E. Hillman, K. A. Siegesmund, and C. R. Dutta. 1967. The primate cerebellar cortex: A Golgi and electron microscopic study. In: *The Cerebellum. Vol. 25. Progress in Brain Research.* Elseiver, New York pp. 174-225.

Glickstein, M., W. Calvin, and R. W. Doty. 1966. Laminar structure of the dorsal lateral geniculate body of *Saimiri* and *Tupaia.* Anat. Rec. 154:348.

Glickstein, M. 1967. Laminar structures of the dorsal lateral geniculate nucleus in the tree shrew *(Tupaia glis)*. J. Comp. Neur. 131:93-102.

Grant, G. 1962. Spinal course and somatotopically localized termination of the spinocerebellar tracts. An experimental study in the cat. Acta Physiol. Scand. 56: suppl 193:5-61.

Haddara, M. A., and M. A. Nooreddin. 1966. A quantitative study on the postnatal development of the cerebellar vermis of mouse. J. Comp. Neur. 128:245-254.

Haines, D. E., K. R. Holmes, and J. A. Bollert. 1968. The extrinsic eye muscles of a prosimian primate *(Galago senegalensis)*. Anat. Rec. 160:358.

_____ 1969. The extrinsic eye muscles of a prosimian primate: Eye muscles of monkey and man. Mich. Acad. (in press).

Hall-Craggs, E. C. B. 1965. An analysis of the jump of the lesser *Galago (Galago senegalensis)*. J. Zool. 147:20-29.

Hill, W. C. O. 1953. *Primates, Comparative Anatomy and Taxonomy I-Strepsirhini*. Edinburgh University Press, Edinburgh.

_____ 1955. *Primates, Comparative Anatomy and Taxonomy. II Haplorhini: Tarsioidea*. Edinburgh University Press, Edinburgh.

Hines, M. 1929. The brain of *Ornithorhynchus anatinus*. Philo. Trans. Toy. Soc. Lond. ser B. 217:155-288.

Hoffman, H. H. 1964. Discussion. In: Quantitative comparisons of brain structures from Insectivores to Primates. H. Stephan and O. J. Andy. 1964. Am. Zool. 4:59-74.

Holloway Jr., R. L. 1968. The evolution of the primate brain: some aspects of quantitative relations. Brain Res. 7:121-172.

Holmes, K. R., D. E. Haines and J. A. Bollert. 1968. Laboratory observations on a prosimian primate *(Galago senegalensis)*. Lab. Animal Care 18:475-477.

Jane, J. A., C. B. G. Campbell, and D. Yashon. 1965. Pyramidal tract: a comparison of two prosimian primates. Sci. 147:153-155.

Jansen, J. 1933. Experimental studies on the intrinsic fibers of the cerebellum. I. The arcuate fibers. J. Comp. Neur. 57:369-400.

_____ 1950. The morphogenesis of the cetacean cerebellum. J. Comp. Neur. 93:341-400.

Jansen, J. and A. Brodal. 1940. Experimental studies on the intrinsic fibers of the cerebellum. II. The corticonulear projection. J. Comp. Neur. 73:267-321.

Jones, R. M. 1964. *McClung's Handbook of Microscopical technique.* Hafner Publ. Co., New York pp. 364-370.

Kanagasuntheram, R. and Z. Y. Mahran. 1960. Observations on the nervous system of the lesser bushbaby. *(Galago senegalensis senegalensis).* J. Anat. 94:512-527.

Krishnamurti, A. 1966. The external morphology of the brain of the slow loris *Nycticebus coucang coucang.* Folia primat. 4:361-380.

Kluver, J. and E. Barrera. 1953. A method for the combined staining of cells and fibers in the nervous system. J. Neuropath. and Exp. Neurol. 12:400-403.

Larsell, O. 1935-36. The development and morphology of the cerebellum in the opossum. Part I. Earul development. J. Comp. Neur. 63:65-94.

_____ 1936a. Cerebellum and corpus pontobulbare of the bat *(Myotis).* J. Comp. Neur. 64:275-302.

_____ 1936b. The development and morphology of the cerebellum in the opossum. Part II. Later development and adult. J. Comp. Neur. 63:251-291.

_____ 1947a. The development of the cerebellum in man in relation to its comparative anatomy. J. Comp. Neur. 87:85-129.

_____ 1947b. The cerebellum of myxinoids and petromyzonts, including developmental stages in the lampreys. J. Comp. Neur. 86:395-445.

_____ 1952. The morphogenesis and adult pattern of the lobules and fissures of the cerebellum of the white rat. J. Comp. Neur. 97:281-356.

_____ 1953. The cerebellum of the cat and the monkey. J. Comp. Neur. 99:135-199.

Larsell, O. and J. Jansen. 1967. *The Comparative Anatomy and Histology of the Cerebellum from Myxinoids through Birds.* University of Minnesota Press, Minneapolis pp. 217-273.

Le Gros Clark, W. E. 1924. On the brain of the tree shrew *(Tupaia minor)*. Proc. Zool. Soc. 1053-1074.

_____ 1925. On the skull of *Tupaia*. Proc. Zool. Soc. 559-567.

_____ 1926. The anatomy of the pen-tailed tree shrew *(Ptilocercus lowii)*. Proc. Zool. Soc. 1190-1307.

_____ 1928. On the brain of the macroscelididae *(Macroscelides* and *Elephantulus)*. J. Anat. 62:245-275.

_____ 1931. The brain of *Microcebus murinus*. Proc. Zool. Soc. 463-489.

_____ 1932. The brain of the Insectivora. Proc. Zool. Soc. 975-1013.

_____ 1959. *The Antecedents of Man*. Edinburgh University Press, Edinburgh.

Marsden, C. D. and R. Towland. 1965. The mammalian pons, olive and pyramid. J. Comp. Neur. 124:175-188.

Miale, I. L., and R. L. Sidman. 1961. An autoradiographic analysis of histogenesis in the mouse cerebellum. Exp. Neurol. 4:277-296.

Miller, M., G. C. Christensen, and H. E. Evans. 1964. *Anatomy of the Dog*. W. B. Saunders Co., Philadelphia pp. 501-524.

Mugnaini, E. and P. F. Forstronen. 1965. The Golgi epithelial cells and the relationships to Purkinje cells. An electron microscopical study on the chick embryo. *Abstracts, 8th Int. Cong. Anat., Wiesbaden*. Georg Thieme Verlag, p. 84.

Mussen, A. T. 1967. *The Cerebellum and Red Nucleus*. Hafner Publishing Co., Inc., New York pp. 47-124.

Napier, J. R. and P. N. Napier. 1967. *Handbook of Living Primates*. Academic Press, New York pp. 330-339.

Nieuwenhuys, R. 1967. Comparative anatomy of the cerebellum. In: *The Cerebellum. Vol. 25. Progress in Brain Research*. Elseiver, New York pp. 1-93.

Nyberg-Hansen, R. 1964. Origin and termination of fibers from the vestibular nuclei descending in the medial longitudinal fasciculus. An experimental study with silver impregnation methods in the cat. J. Comp. Neur. 122:355-367.

Obenchain, J. B. 1925. The brains of the South American marsupials *Caenolestes* and *Orolestes*. Chicago Field Mus. of Nat. Hist. Zool. Ser. 14:175-232.

Oscarsson, O. 1965. Functional organization of the spino- and cuneocerebellar tracts. Physiol. Revs. 45:495-522.

Penfield, W. 1932. Neuroglia: normal and pathological. Cytology and Cellular Pathology of the Nervous System, W. Penfield, Ed. New York, Hoeber, Vol. 2, pp. 423-479.

Reighard, J. and H. S. Jennings. 1940. *Anatomy of the Cat.* Henry Holt and Co., New York pp. 339-369.

Scheibel, M. E. and A. B. Scheibel. 1954. Observations on the intracortical relations of the climbing fibers of the cerebellum. A. Golgi study. J. Comp. Neur. 101:733-763.

Singer, M. 1962. *The Brain of the Dog in Section.* W. B. Saunders Co., Philadelphia.

Snider, R. S. 1940. Morphology of the cerebellar nuclei in the rabbit and cat. J. Comp. Neur. 72:399-415.

Snyder, M. and I. T. Diamond. 1968. The organization and function of the visual cortex in the tree shrew. Brain, Behav. Evol. 1:244-288.

Stephan, H. and O. J. Andy. 1964. Quantitative comparisons of brain structures from insectivores to primates. Amer. Zool. 4:59-74.

Stephan, H., and R. Bauchot. 1965. Hirn-Korpergewichtsbeziehungen bei den Halbaffen (Prosimii). Acta Zoologica 46:209-231.

Tigges, J. 1964. On the visual learning capacity retention and memory in *Tupaia glis* (Diard 1820). Folia primat. 2:232-245.

_____ 1966. Ein experimentellar Beitrag zum subkortikalen optischen System von *Tupaia glis*. Folia primate. 4:103-123.

Tigges, J., B. A. Brooks and M. R. Klee. 1967. ERG recordings of a primate pure cone retina *(Tupaia glis)*. Vision Res. 7:553-563.

Tilney, F. 1927. The brain stem of *Tarsius:* A critical comparison with other primates. J. Comp. Neur. 43:371-432.

Van Hoevell, J. L. D. 1916. The phylogenetic development of the cerebellar nuclei. Proc. Acad. Sci. (Amsterdam) 18:1421-1434.

Van Valen, L. 1965. **Treeshrews**, primates, and fossils. Evolution 19:137-151.

Verhaart, W. J. C. 1966. The pyramidal tract of *Tupaia* compared to that in other primates. J. Comp. Neur. 126:43-50.

Voogd. J. 1967. Comparative aspects of the structure and fibre connexions of the mammalian cerebellum. In: *The Cerebellum Vol. 25. Progress in Brain Research.* Elseiver, New York pp. 94-134.

Voris, H. C. and N. L. Hoerr. 1932. The hindbrain of the opossum, *Didelphis virginiana.* J. Comp. Neur. 54:277-355.

Woollard, H. H. 1925. The anatomy of *Tarsius spectrum.* Proc. Zool. Soc. Pt. 2:1071-1184.

Zeman, W. and J. R. M. Innes. 1963. *Craigies Neuroanatomy of the rat.* Academic Press. New York pp. 85-101.