THE EXTERNAL MORPHOLOGY OF THE BRAIN OF *SEMNOPITHECUS ENTELLUS*

(A Comparative Study)

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Received October 29, 1941
(Communicated by Prof. A. Subba Rau)

Introduction

Consequent on a study of the brains of some of the old world monkeys including *Nasalis*, *Colobus* and *Cynopithecus* with reference to the exhaustive work of Kukenthal and Zichen on the Primate brain, Beddard (1903) makes the following statement: " I cannot distinguish by any tangible differences the arrangement of the furrows in the genera *Macacus*, *Cercopithecus*, *Cercocebus* and perhaps *Papio*. It appears to me that among the Cercopithecidæ there are only two plans of cerebral conformation, one confined to Cercopithecinæ and the other to Semnopithecinæ." It is proposed in this paper to develop this idea further, by a more detailed study of the external morphology of typical representatives of these two subfamilies. The author's own observations on two brains of *Semnopithecus entellus* form the basis for the comparison. Both these brains were practically alike in their topographical details. The description of the brains of *Macacus* and other monkeys have been taken from studies by Elliot Smith (1902), Beddard (1903), Duckworth (1915), Tilney (1928) and Hines (1933); and in addition a personal examination has been made of the brain of *Macacus sinicus*.

General Features of the Brain of Semnopithecus entellus

Viewed from above the entellus brain has a broad oval outline with the narrow end forwards. The cerebellum is completely hidden by the cerebrum. The frontal pole is narrow; the occipital poles are full and rounded. The orbital surface shows the characteristic keel, medially, and hollow, laterally. The inferior surface of the cerebrum is not as deeply moulded by the cerebellum as in *Macacus*. The broadest part of the brain corresponds to the region behind the upper part of the parallel sulcus. On the medial surface of the sagittal section the relatively large corpus callosum is well made out. The continuity between the septum pellucidum and the gyrus subcallosus (parts of the original paraterminal body) is seen (Text-Fig. 2 B) and a flattened band of nervous tissue passes downwards from the lower part of the septum pellucidum in front of the anterior commissure to become the diagonal band of Broca.

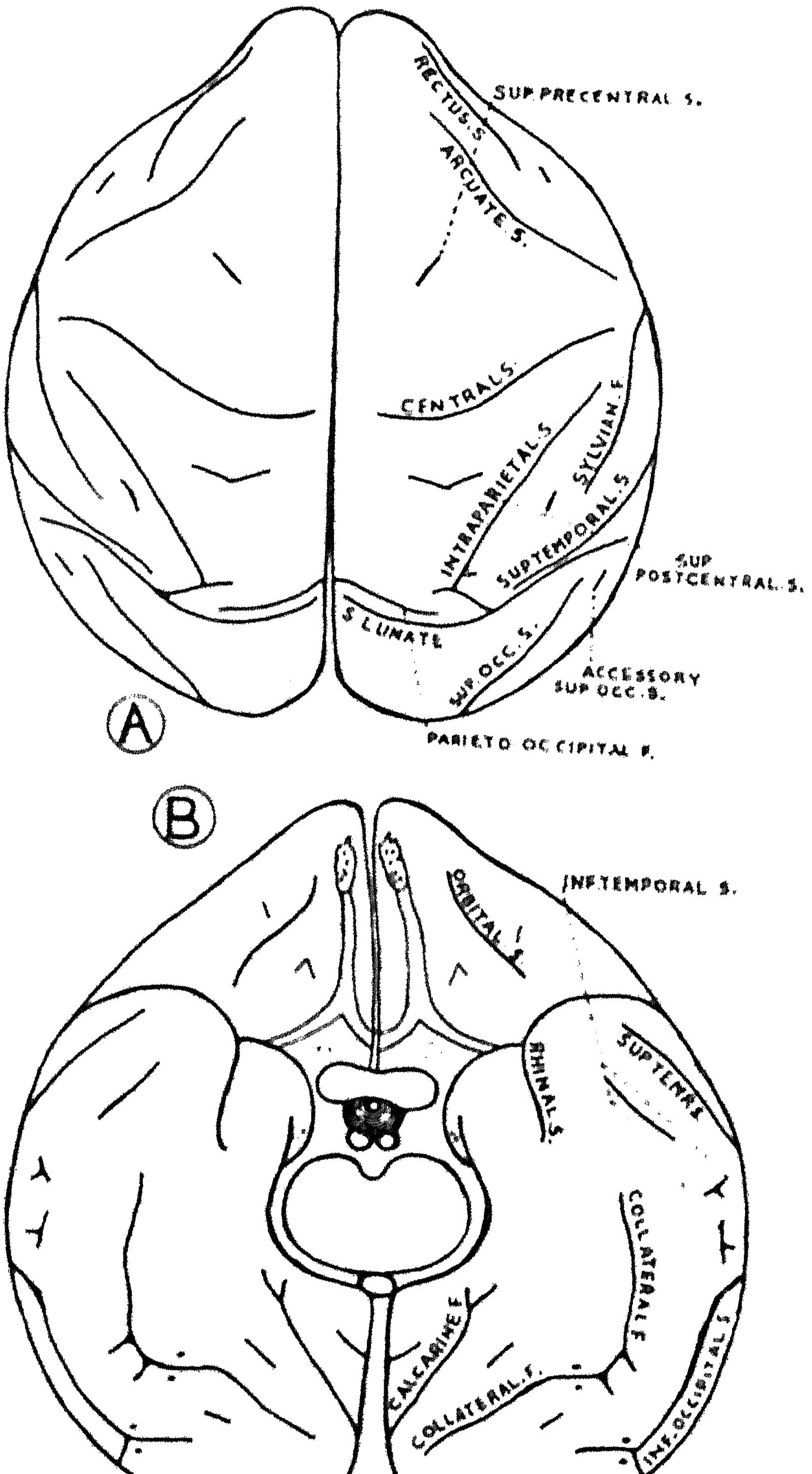
Measurements of the Brain of a Young Adult Female Entellus Monkey

Maximum length of brain	6·85 cm.
Maximum width of brain	5·95 ,,
Encephalic index	87
Length of corpus callosum	3·05 cm.
Thickness of corpus callosum at splenium	0·4 ,,
Precallosal length, *i.e.*, the distance between the genu and frontal pole	1·6 ,,
Postcallosal length, *i.e.*, the distance between the splenium and occipital pole	2·35 ,,
Vertical measurement of anterior commissure	0·3 ,,
Antero-posterior measurement of anterior commissure ..	0·2 ,,
Weight of brain, with meninges immediately after removal	114 gm.
Weight of brain, without meninges and vessels after prolonged hardening in 5 per cent. formalin	86·5 ,,
Weight of forebrain	73·5 ,,
Weight of midbrain	0·75 ,,
Weight of hindbrain	12·25 ,,
Proportions of forebrain: midbrain: hindbrain	85: 1: 14

Fissuration of the Cerebrum in Entellus

The superolateral surface (Text-Figs. 1 A, 2 A)

The central sulcus extends downwards and slightly forwards from a point near the middle of the medial margin and finally makes a terminal bend backwards. The length of the central sulcus is 3·0 cm. On the surface of the cerebrum in front of the central sulcus three sulci are seen, *viz.*, s. rectus, s. arcuatus and s. precentralis superior. The *sulcus rectus* is nearly parallel to the inferior border near the frontal pole and is 1·9 cm. long. The *sulcus arcuatus* is 2·5 cm. long and has a course directed from below upwards and forwards. The arcuate nature is such that in the lower part it runs in a nearly coronal direction and then terminates anteriorly in a nearly sagittal direction. The *superior precentral sulcus* is a small one in front of the upper part of the central sulcus.

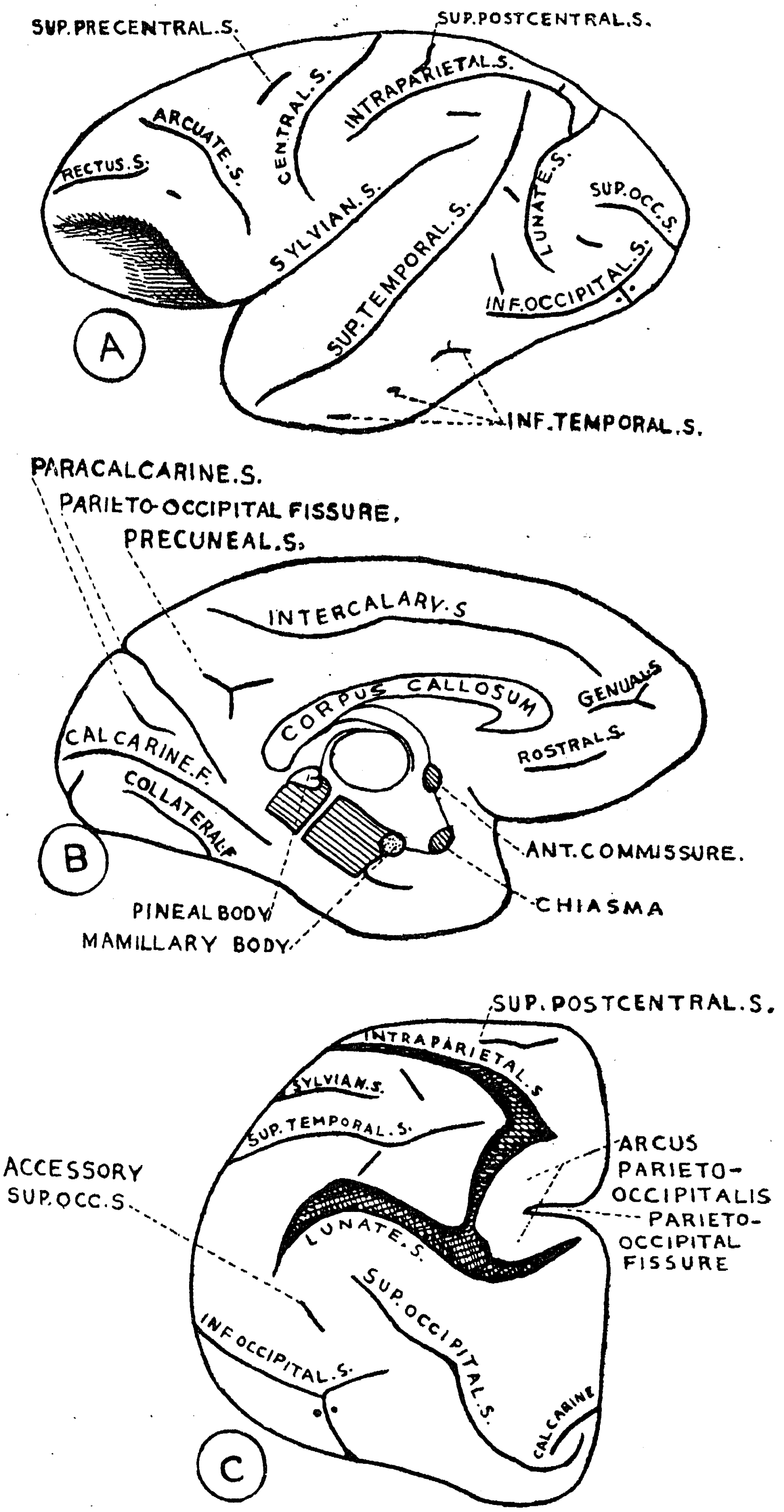


TEXT-FIG. 1. Superior (A) and Inferior (B) views of the cerebral hemispheres

The *Sylvian fissure* has a general oblique direction from below upwards and backwards. Posteriorly its terminal part does not unite with any other sulcus. On opening the lips of the anterior part of the Sylvian fissure the insula is seen. The submerged part of the insula is bounded above by the *suprasylvian fissure*, whose anterior end extends forwards on the deep aspect of the operculum, but is not visible on the superficial surface. A *pseudo-sylvian fissure* limits the insula below. The anterior limiting sulcus of the insula (s. fronto-orbitalis) is absent and the insula becomes continuous with the posterior part of the orbital surface without any line of demarcation. Parallel to Sylvian fissure but more extensive than it inferiorly as well as superiorly is the *superior temporal sulcus* (parallel fissure). It does not join any other sulcus. The *inferior temporal sulcus* is represented by three small detached sulci near the lower part of the temporal lobe. The middle one is the smallest, being just a dimple.

The *intraparietal sulcus* starts midway between the central sulcus and Sylvian fissure and passes at first obliquely upwards and backwards arching over the upper ends of the Sylvian fissure and superior temporal sulcus; the intraparietal then gives off a short medially directed transverse branch in front of the arcus parieto-occipitalis; then turning downwards and backwards the intraparietal joins the lunate sulcus. The *sulcus postcentralis superior* is seen as a coronal sulcus parallel to and behind the upper part of the central sulcus. In the inferior parietal lobule in the region between the intraparietal sulcus above, the posterior part of the Sylvian fissure below and the superior temporal sulcus behind is a small distinct sulcus of doubtful identity whose significance will be discussed subsequently.

The *lunate sulcus* does not touch the superomedial or inferolateral borders. It comes close to the superomedial border but is separated by a considerable interval from the inferolateral border. The sulcus is concave forwards in its upper part and convex forwards in its lower part. The superomedial portion of the lunate sulcus forms the posterior boundary of the arcus parieto-occipitalis. The intraparietal sulcus joins the lunate nearly a third of the way down from its upper end. The lower portion of the sulcus lunatus and the superior temporal sulcus come close to each other but are distinctly separated by a gyrus on whose surface a short unidentified antero-posterior sulcus is seen. The *inferior occipital sulcus* forms a curve concave upwards situated about midway between the lower end of the lunate sulcus and the inferolateral border. The posterior end of the inferior occipital sulcus has the appearance of being bifurcated. The upper limb of the bifurcation, which is the real continuation of the sulcus, passes on to the lateral surface of the occipital lobe. The lower limb of the bifurcation is, however, deeply separated from the rest of the sulcus by a submerged gyrus indicated by two dots in the course of the sulcus in the figures. This deeply detached sulcus passes medially towards the inferior surface. Its significance will be discussed along with the collateral sulcus. In the region situated between the superior temporal sulcus in front, the lunate sulcus behind and the



TEXT-FIG. 2. Lateral (A), Medial (B) and Posterior (C) views of the left cerebral hemisphere. The posterior view is drawn on a higher magnification and the lips of the lunate sulcus and intraparietal sulcus are represented slightly opened out. The arcus parieto-occipitalis is seen fully exposed.

inferior occipital sulcus below, is an unidentified sulcus having a coronal direction. The significance of this sulcus will also be discussed subsequently. The lateral surface near the occipital pole shows the *superior occipital sulcus* and another small sulcus probably accessory to it.

The medial surface (Text-Fig. 2 B)

In the circumcallosal zone on the medial surface the following sulci are seen: (1) a *rostral sulcus* situated midway between the rostrum of the corpus callosum and the medial orbital border, (2) a *genual sulcus* in front of the genu of the corpus callosum, and (3) an *intercalary sulcus* starting above the genual sulcus and passing at first backwards parallel to the upper surface of the corpus callosum and finally taking an obliquely upward course towards the superomedial border. The termination of the upturned part of the intercalary is situated along the superomedial border about midway between the superior postcentral sulcus and parieto-occipital fissure.

In the region corresponding to the precuneus, there is a triradiate *precuneal sulcus* (compensatory sulcus) placed above the splenium of the corpus callosum. It consists of a horizontal element and a vertical element.

The *parieto-occipital fissure* is a deep cleft beginning on the medial surface a little behind the splenium and directed upwards and backwards. It does not meet the calcarine fissure inferiorly, being separated from it by a gyrus. The upper end of the parieto-occipital fissure cuts the superomedial border and extends on to the lateral surface where it is bounded by the well-marked arcus parieto-occipitalis (Text-Fig. 2 C). The arcus is limited in front by a transverse limb of the intraparietal, laterally by the posterior part of the intraparietal and posteriorly by the medial part of the lunate sulcus. On opening the lips of the parieto-occipital fissure the fossa shows hidden in its depth a sulcus placed in relation to its floor along the anterior wall and another very small sulcus on its posterior wall. Posterior to the parieto-occipital fissure is a small sulcus on the cuneus, probably a *paracalcarine sulcus*.

The *calcarine fissure* begins on the medial surface near the occipital pole above the superior occipital sulcus and then runs forwards and downwards on to the inferior surface. It is a deep single sulcus and shows no bifurcation posteriorly and no hidden gyrus in its depth.

The inferior surface (Text-Fig. 1 B)

The *rhinal fissure* extends backwards from the incisura temporalis and forms a lateral boundary to the pyriform area. The *Collateral fissure* begins posteriorly near the occipital pole and runs forwards for nearly two-thirds of the length of the occipitotemporal part of the inferior surface. There is a submerged gyrus in its depth behind its middle showing that it is constituted of two united sulci. It also shows two laterally directed rami from the hinder part of the anterior segment. Mention has already been made in the description of the inferior occipital sulcus of a small sulcus apparently united to its posterior part but deeply separated from it by a submerged gyrus. Between this small sulcus and the collateral fissure is another small detached sulcus. These two small sulci together probably represent the *transverse collateral sulcus.* Between the collateral sulcus and the anterior end of the calcarine fissure a small sulcus is present. This is probably the beginning of a *paracollateral sulcus.* The orbital part of the inferior surface shows a gently curved S-shaped sulcus, the *orbital sulcus,* along with small accessory dimples laterally and medially. The *sulcus olfactorius* is absent.

Comment on Cerebral Fissuration

Inferior parietal lobule.—Even without going into a detailed consideration of the areas of cortical localization and cytoarchitectonics, it will be generally admitted that the inferior parietal lobule, *i.e.*, the region roughly between the intraparietal sulcus in front and above, and the sulcus lunatus behind, is an association area where sensory impressions of touch, hearing and vision are pooled together. The separation of the terminal part of the Sylvian fissure and superior temporal sulcus that occurs in entellus indicates an expansion of this cortical area. In addition certain new sulci have appeared in this region. (1) A small sulcus has appeared between the intraparietal sulcus and posterior part of the Sylvian fissure. It is the superior parallel sulcus (ascending I of Kappers). This identification is in consonance with the interpretation by Beddard (1903) and Shellshear (1927). Beddard also considers that the existence of this sulcus differentiates the brain of *Semnopithecus* from that of *Nasalis.* (2) The gyrus that separates the lunate sulcus from the superior temporal sulcus has a small sagittal sulcus on it. This is the sulcus prelunatus. (3) In the lower part of the triangular area between the superior temporal, lunate and inferior occipital sulci, there is a sulcus in the coronal plane (see Text-Fig. 2 A). This is probably the beginning of an anterior occipital sulcus (ascending III of Kappers). The separation of the Sylvian fissure from the superior temporal sulcus and the appearance of these three sulci in the inferior parietal lobule of the *Semnopithecus* for the first time in the evolution of the Primates are evidences of the expanding growth tendencies of this region.

The intraparietal sulcus.—The transverse branching of the intraparietal in front of the arcus parieto-occipitalis indicates a tendency for the intraparietal to become more complex. The terminal outward bend of the intraparietal sulcus prior to its joining the lunate sulcus is also another feature in which *Semnopithecus* differs from *Macacus.*

The occipital lobe.—The definite decrease in the operculation of the sulcus lunatus and inferior occipital sulcus in *Semnopithecus* as compared with *Macacus*, associated with the constant appearance of a superior occipital sulcus and accessory superior occipital sulcus, shows a backward shifting of the striate area by the expanding peristriate cortex. The formation of the superior occipital sulcus appears to be a means of accommodating " pushed back " striate cortex in the limited space available. Transverse and sagittal sections through the occipital cortex when examined with a hand lens show the stria Gennari extending up to the posterior lip of the lunate sulcus but not extending into the cortex in the depth of the sulcus. The stria Gennari is also made out on the sides of and in the depths of the superior occipital sulcus and the posterior part of calcarine fissure.

The sulcus cinguli.—The sulci that make up the sulcus cinguli of man, *e.g.*, the rostral sulcus, genual sulcus and intercalary sulcus are all present in *Semnopithecus entellus.* But the terminal upturn of the intercalary is situated midway between the superior postcentral sulcus and parieto-occipital fissure and appears to be far too back from the probable posterior limit of the paracentral lobule. It is therefore likely that the terminal part of the intercalary does not correspond to the terminal upturn of the sulcus cinguli of man.

The precuneus.—The precuneus is definitely larger in *Semnopithecus* than in *Macacus.* It is this preponderance of the precuneus over the cuneus that gives a posterior inclination to the parieto-occipital fissure in entellus as contrasted with the upward and forward course of the parieto-occipital fissure in *Macacus.* In Elliot Smith's diagram of the medial surface of the brain of *Macacus sinicus* (fig. 241, *R.C.S. Cat.*, 1902) the precuneal sulcus is absent; and in her diagram of the rhesus brain, Hines (1933) shows a small precuneal sulcus, with a query. On the contrary Duckworth (1915) clearly indicates a compensatory sulcus (sulcus precunei) in *Nasalis* and it it equally well marked in *Semnopithecus entellus.*

The parieto-occipital fossa.—The parieto-occipital fissure is really a complex of submerged sulci, and so it is appropriately called a fossa. The identification of its constituent elements is based on Elliot Smith's interpretation of the parieto-occipital fossa (1902 and 1904). The sulci α, β and γ described and illustrated in fig. 241 of *R.C.S. Cat.* (1902) are named incisura parieto-occipitalis, s. limitans precunei, and s. paracalcarinus, respectively.

In the entellus the incisura parieto-occipitalis occurs separated from the intraparietal by a well-formed arcus parieto-occipitalis and the fossa proper is formed by the submergence within it of the incisura parieto-occipitalis and sulcus limitans precunei, due to an overgrowth of the two lips. The sulcus paracalcarinus, however, is not yet submerged and occurs in the cuneus behind the parieto-occipital fissure. Of the two opercula of the fossa, the anterior operculum seems to show greater growth tendencies than the posterior.

The calcarine fissure.—The posterior T-shaped bifurcation of the calcarine fissure usually seen in *Macacus* is absent in *Semnopithecus entellus.* But it has been occasionally noted in *Semnopithecus* (Beddard, 1903; Elliot Smith, 1902) though not so well visible on the dorsal view of the undivided brain as in *Macacus.*

The collateral fissure.—This fissure is longer and better constituted in *Semnopithecus* than in *Macacus.* It gives evidence of being a union of two sulci, by the presence of a submerged gyrus in its depth. It also shows a tendency to develop two laterally directed rami about its middle. The occurrence of transverse collateral and paracollateral sulci, has already been noted. These are pointers to an expansion of the area around the collateral fissure.

Discussion on Cerebral Fissuration of Semnopithecus entellus

From the foregoing comments on the fissuration of the cerebrum, it becomes clear that the fissural pattern of *Semnopithecus entellus* in addition to being different from what occurs in the Cercopithecinæ is also definitely of a more advanced type. Beddard (1903) suggests from the view-point of cerebral morphology that Colobus "is to be placed with the Cercopithecinæ". The comparison of the brain of *Nasalis* and *Semnopithecus entellus* has already shown that in the formation of the sulcul pattern of the inferior parietal lobule there is a marked advance shown by the entellus monkey. Thus the observations herein noted and the relevant comments made on them lead to the inference that among all the Cercopithecidæ the entellus monkey probably shows the highest cerebral development. In describing the parieto-occipital fissure of *Hylobates hoolock*, Elliot Smith (1902) says: "the series of modifications necessary to convert the brain of a *Macacus* into that of a *Semnopithecus* are carried a stage further in the case of *Hylobates* ". This intermediate position of the *Semnopithecus* between *Macacus* and *Gibbons* is shown by the entellus not only in the region of the parieto-occipital fossa but also in the whole gamut of its cerebral fissuration. More confirmatory evidence will be adduced from the cerebellum and brain stem described below.

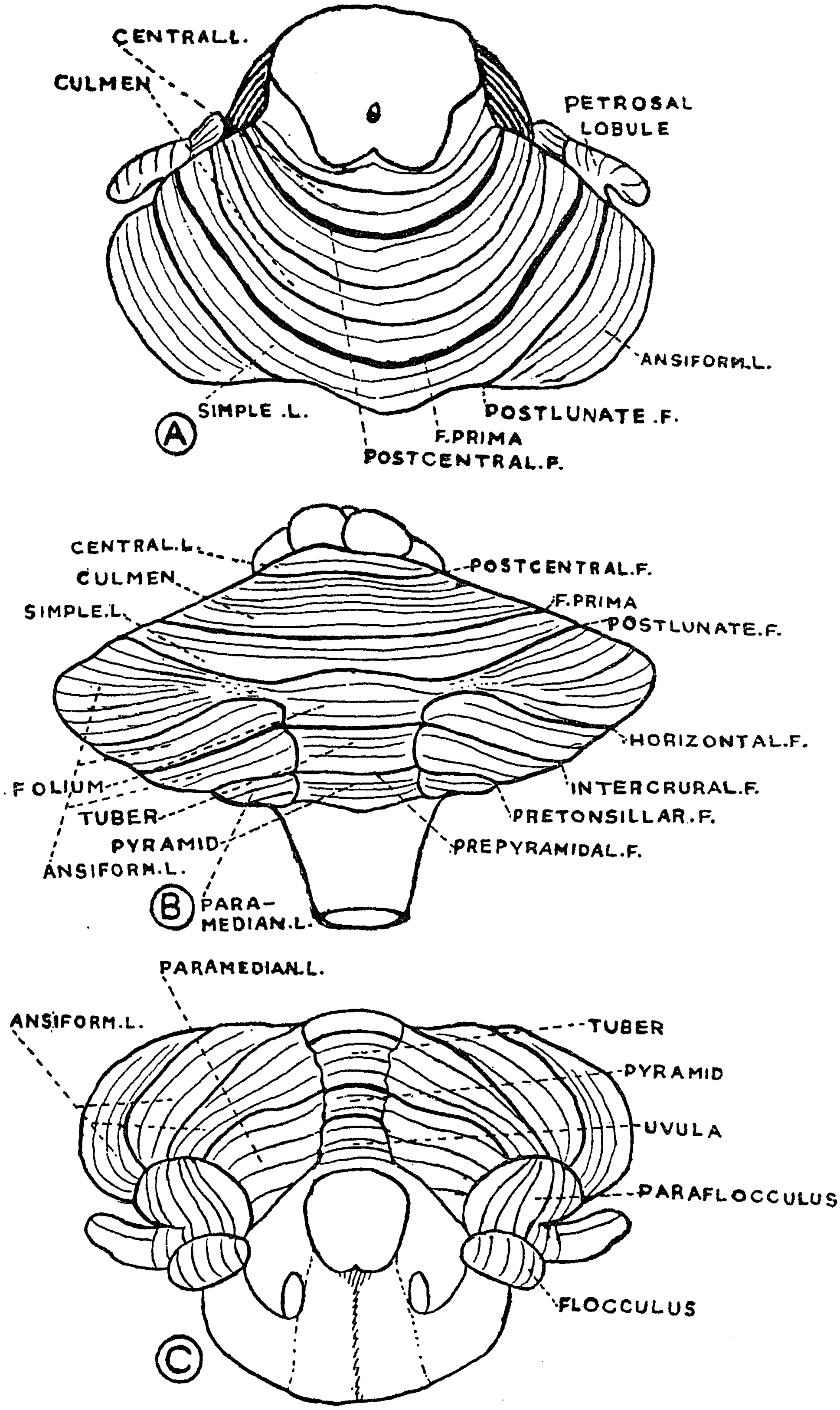
The Cerebellum in Entellus

Nomenclature.—The old nomenclature for the parts of the cerebellum has been purposely ignored. Nor is it considered necessary here to go into a discussion of the nomenclatures according to various authors (Bolk, Ingvar, Elliot Smith, Bradley, Abbie, and Larsell) who have worked on the cerebellum. A summary of the cerebellar subdivisions with the notations of the various nomenclatures used is found in pp. 788–89 of *The Comparative Anatomy of the Nervous System of Vertebrates* (Kappers, Huber and Crosby, 1936). It indicates the complications present. The writer has conveniently adopted the method of subdivision and naming followed by Ranson (1937) in describing the material on hand.

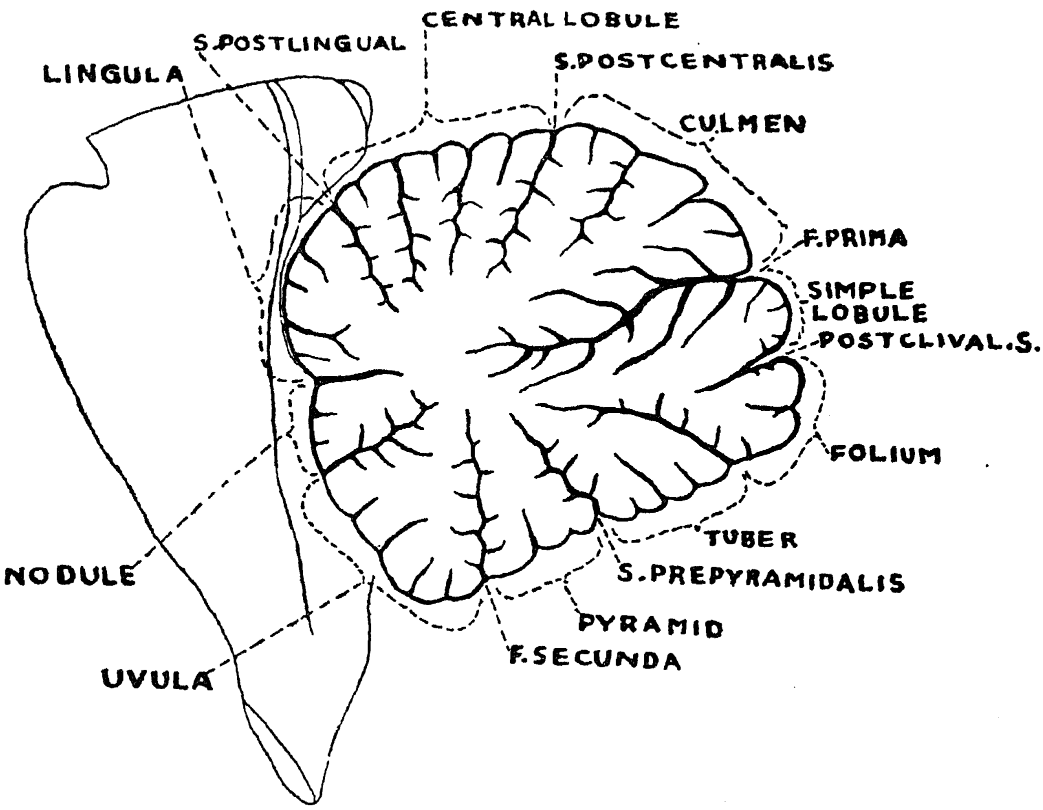
General features (Text-Figs. 3, 4).—The cerebellum of the entellus is 4·3 cm. in transverse diameter and presents the characteristic foliated appearance. The dumb-bell shaped form of the human cerebellum is, however, not present. On viewing it from above, the median part shows a smooth elevation with gentle depressions on either side and the lateral parts bulging out beyond. The three pairs of brachia were as usual.

The anterior lobe (Text-Figs. 3, 4).—The parts in front of the fissure prima, the deepest fissure in the cerebellum, constitute the anterior lobe. On the cut face of the median sagittal section, the anterior lobe appears to be the largest lobe; and its sectional area calculated from a tracing on graph paper is about 48 per cent. of the total sagittal sectional area of the cerebellum. The anterior lobe consists of three subdivisions. (1) The *lingula* comprises five small folia situated on the anterior medullary velum and demarcated from the central lobule by the sulcus postlingualis. (2) The *central lobule* consists of six small folia of which the more caudal ones have expanded laterally. (3) The *culmen* is situated between sulcus postcentralis in front and fissura prima behind. Its median part shows five folia and its expansion on each side forming the anterior quadrangular lobule shows seven folia on the surface. The whole of the anterior lobe is to be considered as a median unpaired structure.

The middle lobe (Text-Figs. 3, 4)—This is bounded in front by the fissura prima and caudally by the sulcus prepyramidalis. It consists of four subdivisions. (1) The *simple lobule* is situated immediately behind the fissura prima. It is also a median unpaired structure though expanding laterally. It shows three folia on its exposed surface. It is limited caudally by the postlunate fissure (post clival sulcus). (2) The *median part* of the rest of the middle lobe includes the folium and tuber, each showing four folia on the exposed surface. (3) The *ansiform lobules* are paired portions of the



TEXT-FIG. 3. Superior (A), Posterior (B) and Inferior (C) views of the cerebellum hemispheres seen partly on superior view (Text-Fig. 3 A) as the expansions external to the postlunate suclus and better seen on posterior and inferior views (Text-Figs. 3 B, 3 C). The ansiform lobules include the superior and inferior semilunar lobules and the biventral lobules. The superior and inferior semilunar lobules are separated from each other by the horizontal fissure. The superior semilunar lobule is larger and shows about nine folia exposed on the surface. The inferior semilunar lobule shows three folia exposed. Caudal to the semilunar lobule is the biventral lobule with the fissura intercruralis as the line of demarcation. The biventral lobules show three exposed folia. (4) The *paramedian lobules* are also paired parts of the middle lobe and are placed caudal to the ansiform lobules, the fissure pre-tonsillaris (retrotonsillaris of some authors) occurring between them. The paramedian lobules correspond to the tonsils.



TEXT-FIG. 4. Median sagittal section of the cerebellum
Drawing was made with camera lucida

The posterior lobe.—This shows two subdivisions: (1) *The median part of the posterior lobe* includes the pyramid and uvula. The pyramid shows three folia and uvula, four surface folia. The pyramid is separated from the uvula by the fissura secunda and uvula from the nodule by the sulcus uvulo-nodularis. The uvula has no lateral extension or connection. But the sides of the cephalic folia of the pyramid apparently show a narrow connecting band between them and the tonsils. (2) *The paraflocculus* forms on each side the lateral parts of the posterior lobe. The paraflocculus is separated from the ansiform and paramedian lobules by the sulcus parafloccularis and from the flocculus by the sulcus flocculoparafloccularis. The paraflocculus shows seven folia on its surface and has a small foliated petrosal lobule prolonged from it.

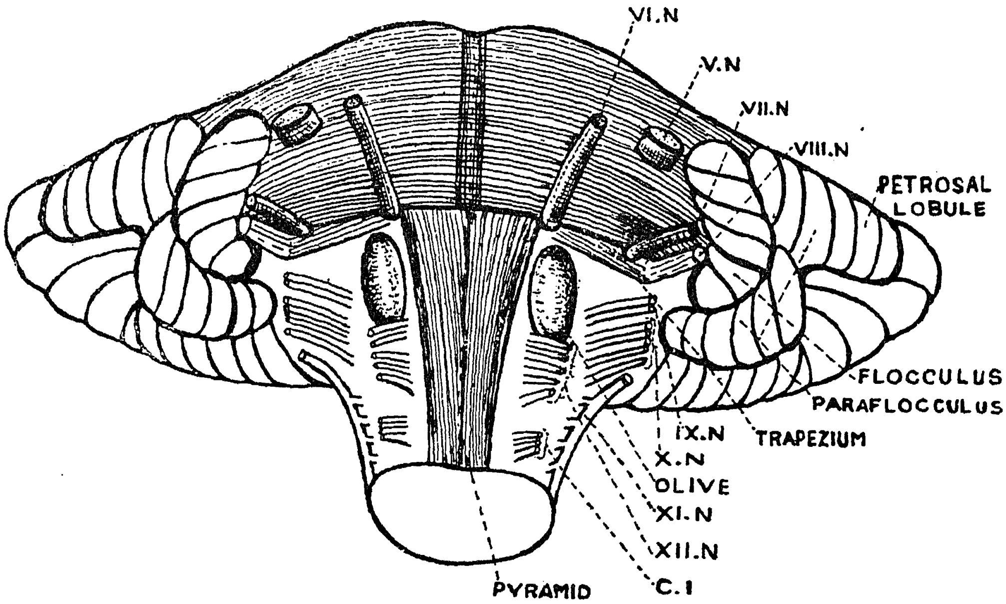
The flocculonodular lobe. This consists of the median part, nodule, showing three surface folia and the paired flocculi showing seven folia on the surface.

Comment on the cerebellum. The cerebellum of entellus shows a better development of the cerebellar hemispheres and a relative smallness of size of the flocculus and paraflocculus compared with *Macacus sinicus* and *rhesus*.

Remarks on the Brain Stem

The anterior commissure of the entellus is relatively smaller than that of *Macacus*. The optic chisma, as in the case of other monkeys, lacks the clear-cut appearance seen in man and appears relatively more bulky. The massa intermedia is a very broad union between the medial surfaces of the two thalami. The pineal body is conical in shape. The corpora mamillaria are distinctly seen as two rounded bodies, whereas in the brain of *Macacus* this division into two is not seen. In the midbrain, the inferior colliculi are smaller, more prominent and slightly more laterally placed. A section through the midbrain shows a large red nucleus. In the floor of the fourth ventricle the stria accoustici are only faintly made out. The colliculus facialis is well marked in the cephalic part of the paramedian eminence. In *Macacus rhesus* the colliculus facialis is not prominent (Hines, 1933). In the lower part of the fourth ventricle, caudal to the trigonum hypoglossi and trigonum vagi, is a posterior funiculus.

The pons is relatively very much larger than that of *Macacus*; and so are the olives and pyramids. Thus there is a greater covering of the corpus trapezoideum by the overlapping posterior border of the pons than occurs in *Macacus* (Text-Fig. 5). The maximum width of the corpus trapezoideum is only 2 mm. in its lateral part. A greater development of the retro-trigeminal part of the pons is indicated by the emergence of the fifth nerve approximately midway between the two borders of the pons. This is a sign of evolutionary advance (Abbie, 1934). The facial and abducent nerves emerge immediately below the pons. The acoustic nerve is an apparent continuation of the corpus trapezoideum.



TEXT-FIG. 5. Ventral view of pons, medulla and upper part of spinal cord

Summary and Conclusions

The brain of the Indian langur, *Semnopithecus entellus* is described. The following are some of the significant observations resulting from a comparative study.

(1) The cerebrum of *Semnopithecus entellus* compared with that of *Macacus* shows a less moulding of its inferior surface by the cerebellum.

(2) The proportions of the weights of forebrain to midbrain to hind-brain are 85 : 1 : 14 in *Semnopithecus entellus* and according to Tilney (1928), 84 : 2 : 14 in *Macacus rhesus.*

(3) In its cerebral fissuration, especially in the regions of the inferior parietal lobule, occipital lobe, precuneus, parieto-occipital fossa, and collateral fissure, *Semnopithecus entellus* shows an intermediate stage between the other Cerecopithecidæ and *Hylobates.*

(4) In the cerebellum of the langur there is a relatively greater development of the hemispheres and a lesser size of the flocculus and paraflocculus when compared with *Macacus.*

(5) The entellus has larger olives, pyramids and pons and the corpus trapezoideum is covered over by the retro-trigeminal part of the pons to a greater extent than in *Macacus.*

(6) This study of external morphology indicates that *Semnopithecus entellus* has probably the most advanced brain among the Cercopithecidæ. A study of its internal structure is likely to be an extremely valuable addition to our knowledge of the Primate brain.

Acknowledgement

It is a pleasure to express my deep indebtedness to Dr. U. V. Nayak, for his invaluable help and criticism and my thankfulness to Miss Chacko for facilities to examine the specimen of brain of *Macacus sinicus* on which she is working.

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