THE ASCENT OF PREHISTORIC MAN

MAN'S CULTURAL STAGES AND PHYSICAL DEVELOPMENT TO THE END OF THE OLD STONE AGE

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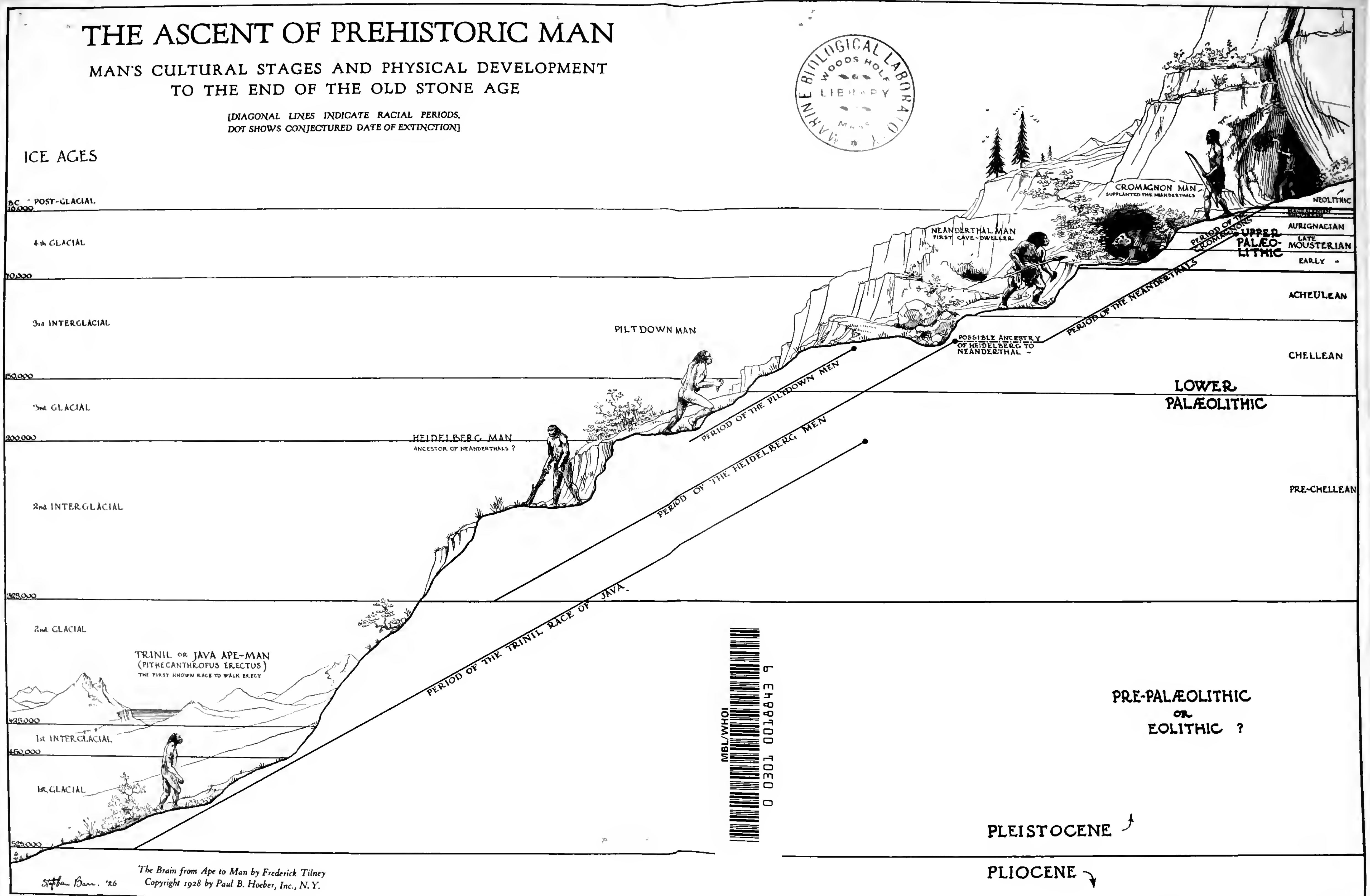

THE BRAIN
FROM APE TO MAN

THE BRAIN FROM APE TO MAN

A CONTRIBUTION TO THE STUDY OF THE EVOLUTION AND DEVELOPMENT OF THE HUMAN BRAIN

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WITH CHAPTERS ON THE RECONSTRUCTION OF THE GRAY MATTER IN THE PRIMATE BRAIN STEM BY

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557 ILLUSTRATIONS, MANY IN COLOR

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INTRODUCTION TO PART III

THE great man-like apes have acquired an especial interest because of widespread notoriety aroused by them as the supposed forebears or direct ancestors of man. This reputation has created an attitude toward the anthropoids which has not always redounded to their credit. Indeed, it often has inspired the eloquence of sentimental tirades, for which they have been the quite undeserving objects. And yet, in such a number of their structural features and behavioral specializations do they resemble their more exalted neighbors in the human family, that a most unpleasant suspicion still lurks in the minds of many. A strangely persistent feeling exists that there may be some fundamental truth in the alleged simian line of human descent. In some this has produced an almost morbid curiosity concerning the man-like apes. Others, perhaps more scientifically inclined, have assiduously followed the matter in order to satisfy themselves concerning the relation which these great apes bear to the races of man.

At various times and by various authorities, each one of the three great anthropoids has been put in close relation to man. Thus, the orang-outang has been considered the nearest approach to human kind among the anthropoid apes. Such a view was long supported by Sir Richard Owen. Other equally important authorities place the chimpanzee in this close relationship to the human family, while many, like the present writer, believe that this position should be assigned to the gorilla because this animal, especially in the differentiation of the central nervous system, seems to correspond most closely to the human type. All of the great man-like apes, however, have so much in common with their higher coordinate, man, that the question as to which of them is most humanoid becomes somewhat academic. It is probable, moreover, that each of the higher primates, perhaps with the exception of man himself, represents a cul-de-sac in the process of progressive specialization in which each is, as it were, an evolutional terminus. This, however, may not be so strictly the case with man in whom the possibility of further differentiation may have been retained to a certain extent. His future alone must reveal his latent capacity for development, if such there be.

The actual interrelationship between man and the great apes seems much more likely to be based upon derivation from some common or generalized stock which held in it the potentialities to specialize along the anthropoid line in one direction, and through certain subhuman stages to man in another. There are unquestionable differences between the anthropoids and man which justify the opinion of extremely remote kinship at best, even in spite of striking similarities. It would seem most probable that neither modern man nor any of his extinct paleolithic predecessors who have appeared in the human drama may trace a direct line of descent to one or other of the living anthropoid apes. These animals have enlisted so much the attention of many noted scientists that the summary of their behavior given here gains considerably by recounting views already expressed by certain distinguished observers.

The three anthropoid apes are usually included in the family Simiidae, represented by three genera which are arranged according as their species appear to be nearest to man. In this discussion the orang-outang is placed lowest in the scale and consequently farthest away from man. The next position is assigned to the chimpanzee, while for the gorilla is reserved the closest approximation to the human kind. This classification is based largely upon morphological consideration of the brain structure which to the mind of the present writer forms a reliable criterion in assigning to each of these anthropoids its respective place.

Chapter XVII

SIMIA SATYRUS, THE ORANG-OUTANG, ITS BRAIN AND BEHAVIOR

Its Position among the Primates; Measurements and Brain Indices; Surface Markings of the Brain and Brain Stem; Structure of the Brain Stem in Cross Section

If the orang-outang enjoys a reputation less romantic than either of his great congeners, the chimpanzee and the gorilla, this is due to his insular habitat which has left him somewhat inaccessible to the attentions of European curiosity. Whatever fabulous repute he may have among the natives of his island home, he has had less opportunity to fall into the nimble hands of the modern fable-makers. It is particularly fortunate that the story of his life appears to have had its first real introduction to civilization through the auspices of one of the most celebrated of naturalists, Alfred Russell Wallace.

Appearance and Habits of the Orang-Outang

The orang is found only in Borneo and Sumatra, and there seems to be considerable doubt as to whether the animals found in these two localities constitute distinct species. It is the custom for most systems of classification to designate one as the Bornean orang and the other as the Sumatran orang. The adult animal has a heavy body, short thick neck, a round head and somewhat receding forehead, a distinctly protruding muzzle with large mouth, broad lips and face uncovered by hair. The lips are mobile and protrusive. The arms are very long, reaching to the ankles in the upright posture. The hands are long and narrow and the thumb is short. The fingers are united by webs at the base of the proximal phalanges. The legs are short in comparison with the length of the body and considerably bowed. The feet are long and narrow. The great toe is short but opposable. Ischial callosities are sometimes present in the male adult, but the tail is absent. The body is covered with a light brownish hair of considerable length, unlike the hair of the two other great anthropoids, which is darkish. The contrast makes the orang appear light-colored in comparison with the gorilla and chimpanzee. Concerning the height of the orang, Wallace believes that it seldom exceeds four feet two inches, and is on the average about four feet one inch. The outstretched arms measure seven feet two inches to seven feet eight inches. Wallace discounts the report of an orang which approaches in any way near to the stature of the gorilla, although statements to the effect that certain captured specimens have measured five feet three inches have been made by several travelers. The figures given by Wallace coincide with those of the majority of observers and may, therefore, be accepted as the most accurate measurements.

The Dyaks, inhabiting the Island of Borneo, believe that the orang which they call "mias" is possessed of prodigious strength and for this reason is seldom, if ever, attacked by other animals of the forest. It really seems to have no enemies because of its own great offensive power, and only two of the great reptiles even presume to attack it — the crocodile and the python. The orang always succeeds in killing the crocodile by main strength, standing upon its back and opening its jaws until he is able to rip out its throat. If attacked by the python, the orang seizes the reptile with both hands, squeezing it with such force and biting it so ferociously that the outcome of the combat is soon decided in favor of the anthropoid.

WALLACE'S ACCOUNTS OF THE ORANG-OUTANG

The following abstracts are taken from Wallace's interesting account of the orang-outang which appears in his famous "Malay Archipelago":

Courtesy, American Museum of Natural History

FIG. 216. HABITAT GROUP, ORANG-OUTANG, SADONG RIVER, BORNEO.

Courtesy, New York Zoological Garden

FIG. 217. ORANG-OUTANG, IN THE ERECT POSTURE, ILLUSTRATING THE DISPROPORTION OF THE ARMS AND LEGS.

"The animal has a wide distribution, inhabiting many districts along the coast of the island where it appears chiefly confined to the low swampy forests. It particularly affects a country which is low and level with a few

Courtesy, New York Zoological Garden

FIG. 218. ORANG-OUTANG, SHOWING CERTAIN ANTHROPOMORPHOUS TENDENCIES IN THE HEAD AND FACE.

isolated mountains on some of which the Dyaks have settled and planted many fruit trees which are a great attraction to the orang as its most desirable food seems to be the unripe fruit. The actual habitat of the animal is in the lofty virgin forest in which they can roam in every direction with as much facility as the Indian on the prairie, passing from treetop to treetop without being obliged to descend to the earth. The orang makes his way leisurely through the forest with remarkable ease. He walks deliberately along the larger branches in a semi-erect attitude which his great length of arm and the shortness of his legs causes him naturally to assume. The disproportion between his limbs is increased by walking on his knuckles and not on the palm of his hand. He chooses those branches which intermingle with those of the

Courtesy, American Museum of Natural History

FIGS. 219 AND 220. HAND AND FOOT OF THE ORANG-OUTANG.

LEFT. Palmar surface of hand showing long, prehensile type of hand and short, rudimentary thumb. These features are special adaptations to arboreal life.

RIGHT. Plantar surface of the foot showing the great toe in a position about midway between the heel and the other toes. The lesser toes are long, and especially adapted to the clinging grasp necessary to arboreal life. Attention is called to the position of the great toe and the advance toward the ball of the foot which progresses in the next higher apes, chimpanzee and gorilla (see Figs. 247, 248, 284 and 285).

adjoining trees. In approaching these, he stretches out his long arms, seizing the neighboring bough with both hands, and then deliberately swings himself across to the next branch on which he walks along as before. He never jumps or springs nor even appears to hurry himself, yet he manages to get along almost as quickly as a person can run through the forest beneath. The long powerful arms are of the greatest use to the animal as they enable him to climb easily the highest trees, to seize fruits and young leaves from slender boughs which will not bear his weight, and to gather leaves and branches with which to form his nest at night. When wounded, he endeavors to make a nest in which to remain quiet, and similarly, at night, prepares a

Courtesy, American Museum of Natural History

FIGS. 221 AND 222. HAND AND FOOT OF ORANG-OUTANG.

LEFT. Dorsum of hand showing long, tapering fingers, short thumb, and specialization to arboreal life.
RIGHT. Dorsum of the foot showing many hand-like qualities, with the great toe nearer to the heel than the ball of the foot.

resting place in the trees to sleep. He likes this place low down in the trees not over twenty or fifty feet from the ground, probably because in this position it is warm and less exposed to the wind. The orang, it is said, makes a new nest for himself every night, or, perhaps, remakes an old one. In rainy weather the animal covers himself with leaves or large ferns, and this may have led to the belief that he actually builds huts in the trees. The animal does not arise from his bed in the morning until the sun is well up and has dried the dew upon the leaves. His feeding hours extend through the forenoon, and he seldom returns to the same trees two days in succession.

They have no particular fear of man and only retreat slowly after a considerable period of scrutinizing inspection. They do not manifest so much of the gregarious tendency as do the other large apes. Two full-grown animals are seldom seen together, but males and females are sometimes accompanied by half-grown young ones. At other times three or four young animals are seen together. Their food consists almost exclusively of fruits, leaves, buds and young shoots. They seem to prefer the unripe fruit even when very sour or intensely bitter, the red fleshy arillus being a particular favorite. The orang rarely descends to the ground except when pressed by hunger, when it seeks the succulent shoots at the riverside. In very dry weather it also comes down from the trees in quest of water of which it generally finds sufficient in the hollow of the leaves. They have been seen upon the ground playing together, at which times they assume the erect posture and grasp each other with their arms."

Wallace believes that it is safe to say that the orang never stands or walks erect unless when using its hands to support itself by the branches overhead or when attacked; and that the representations of its walking with a stick are quite imaginary.

The account given by Wallace of his experience with a young orang whose mother had been killed the preceding day is interesting because of the many human resemblances it records. For example, the great prehensile strength of this almost helpless orang-outang infant, in hands and feet, was quickly demonstrated by the tenacity with which the explorer's beard was grasped and retained. It was both a prolonged and painful ordeal to get away from the clinging young one. The animal had not a single tooth, but soon its milk teeth began to appear much like a human infant. The lack of milk on the island served as a great embarrassment in feeding the young ape, but when the finger was placed in its mouth it sucked with great vigor, drawing in its cheeks with all its might in a vain effort to extract milk. Only after persevering a long time would it give up in disgust and set up a scream very like that of a baby in similar circumstances. When handled or nursed it was very quiet, and when laid down by itself, it would invariably cry. It enjoyed being rubbed after its morning bath and was quite happy while its hair was being combed and brushed. For the first few days it clung desperately by all four hands to whatever it could lay hold of, and Wallace remarks that it was necessary for him to exert special precautions to keep his beard out of the way. A little hare-lip monkey of the macacus variety was subsequently obtained as a companion for the young orang, and it was curious to observe the different actions of these two young simians, the one the offspring of a great anthropoid and the other of a much lower form of primate. The two young animals were of about the same age, but the orang was very like a baby lying on its back quite helpless, rolling lazily from side to side, stretching out all four hands into the air, wishing to grasp something but hardly able to guide its fingers to any object. When dissatisfied, it opened wide its almost toothless mouth, expressing its wants by a most infantile scream. The little monkey, on the other hand, was in constant motion, running and jumping about wherever it pleased, examining every thing about it, taking hold of objects with the greatest precision, balancing itself on the edge of the box and searching everywhere for something to eat. There could hardly be a greater contrast. The orang behaved in so many ways as a human infant as to give the impression that a long period of slow development was necessary to it. This appeared essential in order that the potential elements of its growth might attain their fullest expression by retarding the period of maturity to a relatively late period.

YERKES' PSYCHOLOGICAL STUDIES

The orang-outang has not been so extensively subjected to exact psychological study as its more capable fellow anthropoid, the chimpanzee.

It is fortunate, however, that at least one of this species has come under the critical observation of a most astute student of animal behavior, Professor Robert M. Yerkes. In his notable contribution on "The Mental Life of

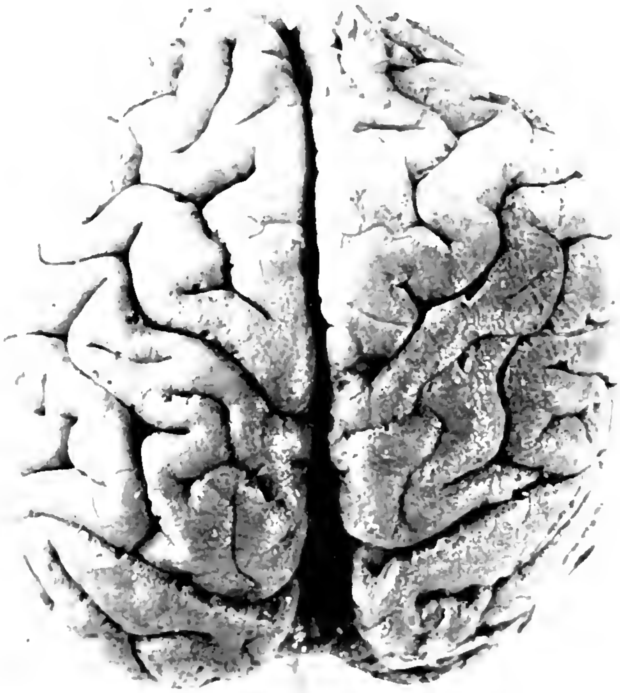


FIG. 223A. DORSAL SURFACE OF BRAIN, ORANG-OUTANG.
[Actual Length 94 mm.]

Monkeys and Apes," Professor Yerkes has described certain tests devised for estimating the intelligence of lower animals, and applied to the partly grown orang, known as "Julius." These tests were designed upon what is known as the *multiple choice basis*. Concerning the results obtained from the orang-outang as compared with other lower primates, Yerkes says that Julius, after many unsuccessful efforts to solve the problem by the method of trial and error lasting for a period of over two weeks, quite unexpectedly one morning seemed to get the idea of what was expected of him and responded to the test without a single mistake. He had seemed to solve the problem sud-

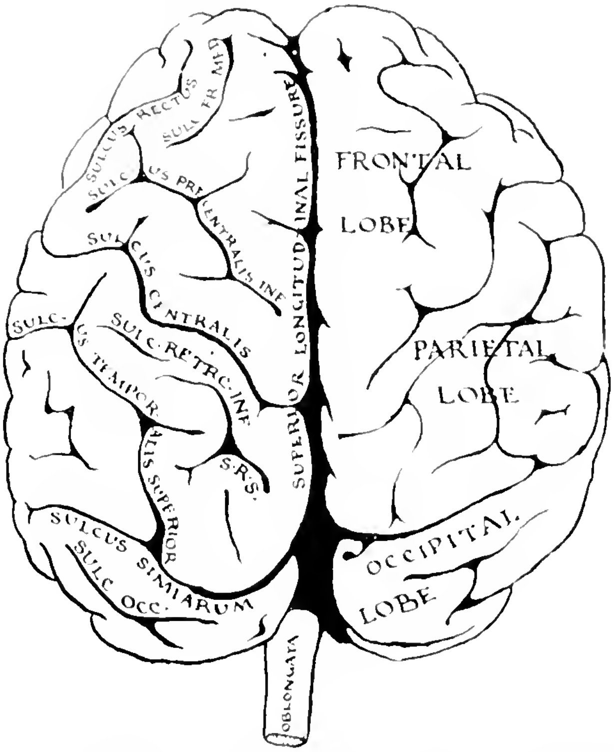


FIG. 223B. DETAILED DIAGRAM OF DORSAL SURFACE OF BRAIN, ORANG-OUTANG.

KEY TO DIAGRAM. SULC. FR. MED., Sulcus Frontalis Medius; SULC. OCC., Sulcus Occipitalis Inferior; SULCUS PRECENTRALIS INF., Sulcus Precentralis Inferior; SULC. RETRC. INF., Sulcus Retrocentralis Inferior; S.R.S., Sulcus Retrocentralis Superior.

denly and in all probability, ideationally. The curve of learning plotted from the daily wrong choices of the animal, had it been obtained from a human subject, would undoubtedly have been described as ideational, possibly even as rational. For its sudden drop from near the maximum to the base line strongly suggests, if it does not actually prove, the presence of insight. Never before has a curve of learning like this been obtained from an infrahuman animal. Yerkes feels justified in concluding from the evidence in hand, which he has presented in extenso in the work referred to, that the orang-outang solves problems set before him ideationally. As a matter of fact, for

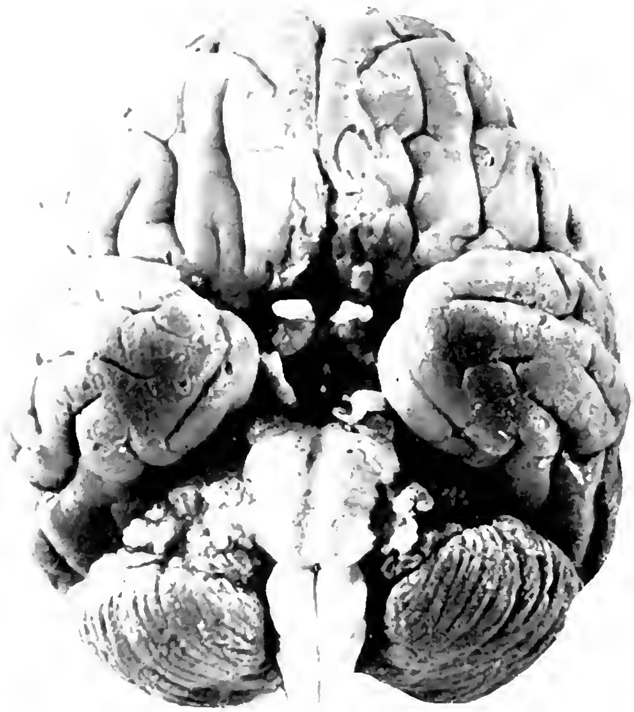


FIG. 224A. BASE OF BRAIN, ORANG-OUTANG.
[Actual Length 94 mm.]

the solution he required about four times the number of trials of several of the lower primates, which, if judged by the number of these trials, would seem to have an intelligence greater than the anthropoids. But other facts clearly indicate that Julius, the orang, is far superior to the monkeys in his intelligence, and suggest that in the animal, ideational learning tended to replace the simpler mode of problem solution by trial and error. For Julius, seemingly incapable of solving his problems by this lower grade process, strove persistently and often vainly to gain insight. It is true, he used ideas defectively at first, but later to much better purpose. Animals far lower in

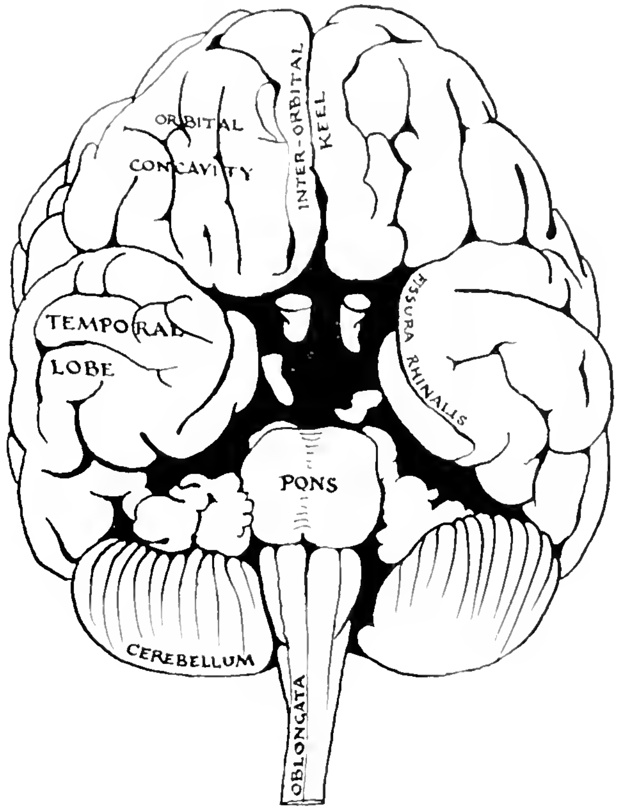


FIG. 224B. DETAILED DIAGRAM OF BASE OF BRAIN, ORANG-OUTANG.

intelligence, for example the pig, surpassed the orang in their ability to solve these relational problems because they used the method of elimination by trial consistently and effectively. Julius, in these experiments, made a poor showing because his substitute for trial and error is only slightly developed, but, nevertheless, sufficiently advanced to bring about the final solution of the problem by ideation.

Measurements and Indices of the Orang-Outang

The cranial measurements of the orang-outang are:

Occipito-nasal diameter	165 mm.
Intertemporal width	88 mm.
Breadth of brain case	98 mm.

The dimensions of the brain, including cerebellum and brain stem, are:

Longitudinal	96 mm.
Transverse	84 mm.

The brain is markedly gyrencephalic with its fissural pattern corresponding closely in detail to that of the human brain.

Total weight of the brain	246 gm.
Total water displacement of the brain	250 c.c.
Weight of the forebrain	213 gm.
Weight of the midbrain	4 gm.
Weight of the hindbrain	29 gm.

The water displacement of the several portions of the brain gave the following results:

Water displacement of the forebrain	219 c.c.
Water displacement of the midbrain	3 c.c.
Water displacement of the hindbrain	28 c.c

On the basis of these figures, the following encephalic indices were computed:

Forebrain index	83 per cent
Midbrain index	5 per cent
Hindbrain index	12 per cent

A forebrain index of 83 per cent allies the orang-outang with the group of animals recognized as having well-advanced manual differentiation, as is the case with all of the primates.

Surface Appearance of the Brain in the Orang-Outang

FISSURES AND LOBES

In pattern the brain of the orang-outang is richly gyrencephalic, its lateral, basal and mesial surfaces presenting many convolutions, the disposition of which almost exactly coincides with that of the human brain. The hemisphere in its occipital portion completely covers the cerebellum. The superior longitudinal fissure at the occipital pole of the hemisphere tends to diverge slightly in order to accommodate the elevation caused by the superior vermis of the cerebellum. This divergence at the caudal extremity of the superior longitudinal fissure is most pronounced in the lower and intermediate primates. It gradually becomes less conspicuous in the higher members of the primate group.

The fissural pattern of the lateral convexity of the cerebral hemisphere is grouped about three main fissures, namely, (1) the fissure of Sylvius, (2) the fissure of Rolando and (3) the semilunar or simian fissure. These fissures determine a distinctly human type of lobation in the hemispheres. The fissure of Rolando, starting about midway between the frontal and occipital poles, at or near the superior longitudinal fissure, extends obliquely downward and forward toward the Sylvian fissure. It presents two genuflexions, both less prominent than in the human brain. By means of this Rolandic fissure, the frontal lobe is separated from the parietal lobe. The Sylvian fissure, somewhat shorter than in man, presents its usual divisions, and upon the lateral surface extends obliquely backward and upward to be surrounded by the marginal convolution at its caudal extremity. It constitutes a boundary between the temporal lobe and the parietal lobe. The sulcus simiarum is prominent and extends from the superior longitudinal sulcus toward the base of the temporal lobe. It separates the parietal from the occipital lobe and forms a boundary between the occipital and temporal lobes. The presence

FIG. 225A. LEFT LATERAL SURFACE OF BRAIN, ORANG-OUTANG.
[Actual Length 96 mm.]

of this simian sulcus, so well defined in the orang, adds a feature to the lateral aspect of the hemisphere usually not present in the human brain. It thus serves as one of the distinguishing marks between man and the anthropoids. Its development in orang has more of the primitive simian character than is the case in either chimpanzee or gorilla. The convolutional pattern of the parietal lobe, as is always the case, shows the greatest richness of gyration, and, in accordance with the rule, the temporal lobe is the next most conspicuous in this particular. The superior temporal sulcus, however, is not continuous into the parietal lobe as in the higher primates; a deep annectent gyre interrupts this sulcus near the base of the temporal region so that it is difficult to identify an angular gyrus. The convolutional pattern in the frontal lobe is relatively rich. The prototype of each fissure found in the human brain is present in orang. This gives the frontal lobe a distinctly humanoid appearance. The proportion between the frontal and parieto-occipito-temporal

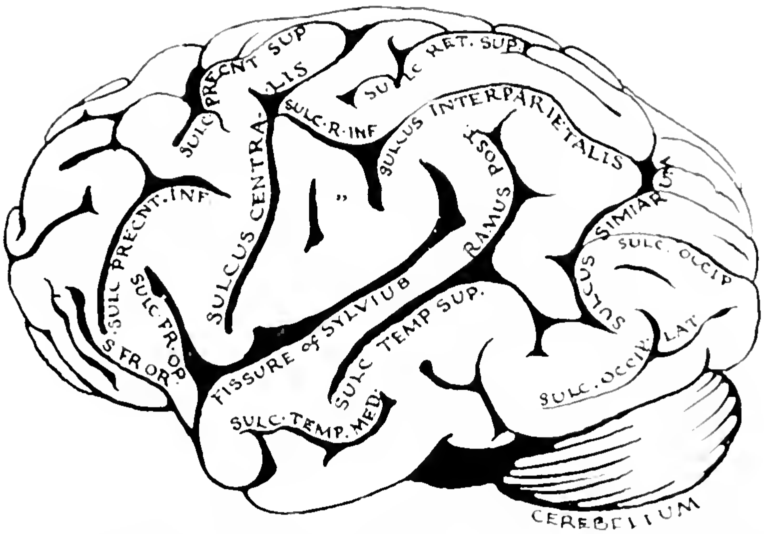


FIG. 225B. DETAILED DIAGRAM OF LEFT LATERAL SURFACE OF BRAIN, ORANG-OUTANG.

KEY TO DIAGRAM. RAMUS POST., Ramus Posterior of Sulcus Temporalis Superior; SULC. FR. OP., Sulcus Fronto-opercularis; S. FR. OR., Sulcus Fronto-orbitalis; SULC. OCCIP., Sulcus Occipitalis; SULC. OCCIP. LAT., Sulcus Occipitalis Lateralis; SULC. PRECNT. INF., Sulcus Precentralis Inferior; SULC. PRECNT. SUP., Sulcus Precentralis Superior; SULC. R. INF., Sulcus Retrocentralis Inferior; SULC. RET. SUP., Sulcus Retrocentralis Superior; SULC. TEMP. MED., Sulcus Temporalis Medius; SULC. TEMP. SUP., Sulcus Temporalis Superior.

areas appears to be about the same as in man. Actual planimetric measurements, however, show a disparity in this regard which favors the frontal area of the human brain. The convolutions of the occipital lobe are fairly rich, but less marked than in any other region. Upon the mesial surface a deep annectent gyre comes to the surface and thus interrupts the direct continuity of the sulcus simiarum with the occipital sulcus. This interruption by means of an annectent gyre in the course of this fissure is a feature frequently found in the brain of the great anthropoids.

The Basal Surface of the Brain

Upon the basal surface of the brain, the hemisphere in the frontal region shows the two characteristic orbital concavities which are fairly well marked

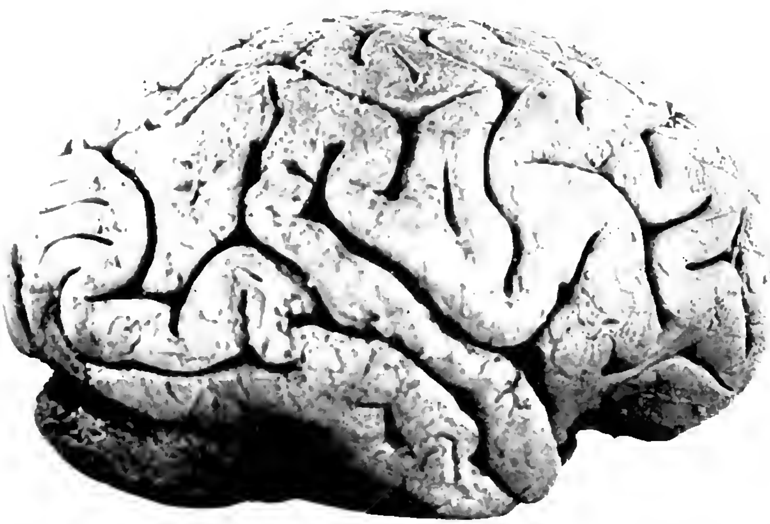


FIG. 226A. RIGHT LATERAL SURFACE OF BRAIN, ORANG-OUTANG.
[Actual Length 96 mm.]

although gradually losing their lateral boundaries. Mesially these concavities are bounded by two marked projections, forming the interorbital keels which are more prominent than in the higher anthropoids and less pronounced than in the lower and intermediate forms. The olfactory bulb and tract are detachable from the orbital surface as far back as the trigonum olfactorium. A small olfactory fissure separates a rudimentary gyrus rectus from the major orbital convolutions. The tip of the temporal lobe is sharply separated from the orbital surface by the horizontal limb of the Sylvian fissure, and presents a fairly well-defined uncus on its mesial surface. In the occipital region the cerebellar concavity is well marked. It is especially pronounced in its median portion where it forms a well-defined postsplenial fossa.

THE CEREBELLUM

The cerebellum is entirely overhung by the occipital surface of the hemispheres. Its tentorial surface is considerably gabled and sharply inclined

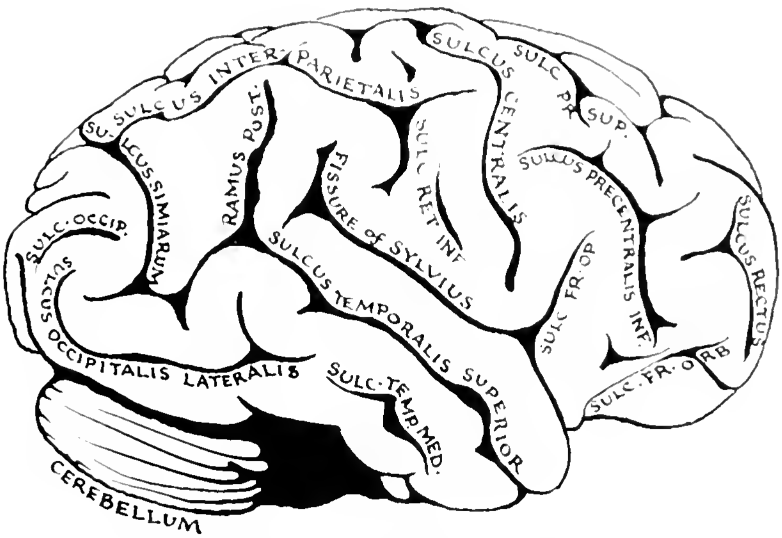


FIG. 226B. DETAILED DIAGRAM OF RIGHT LATERAL SURFACE OF BRAIN, ORANG-OUTANG.

KEY TO DIAGRAM. RAMUS POST., Ramus Posterior of Sulcus Temporalis Superior; SULC. FR. OP., Sulcus Fronto-opercularis; SULC. FR. ORB., Sulcus Fronto-orbitalis; SULC. OCCIP., Sulcus Occipitalis, SULC. PR. SUP., Sulcus Precentralis Superior; SULC. RET. INF., Sulcus Retrocentralis Inferior; SULC. TEMP. MED., Sulcus Temporalis Medius.

toward a fairly defined median ridge-pole which forms the superior cerebellar vermis. This central portion is more prominent at its cephalic extremity which projects into the postsplenial fossa on the undersurface of the hemispheres. The posterior cerebellar notch on the occipital surface is clearly defined but less marked than in the chimpanzee, gorilla or man. The inferior vermis, which is easily discerned upon this surface, does not lie in a depression so deep as the vallecula of the human, chimpanzee or gorilla brain. Upon the tentorial surface the sulcal lines are continued without interruption from the vermis to the lateral lobes, while two paramedian sulci interrupt the course of the folial sulci on the occipital surface. In their lateral expansion, the occipital surfaces of the lateral lobes are neither so broad nor so long as in the case of the still higher primates. There is, however, a decided advance in all of these respects as compared with the lower and intermediate primates. The petroso-ventricular surface of the cerebellum shows no departure from the conditions observed in the lower forms. A relatively small flocculus occupies the cerebello-pontile angle into relation with which also enters a large middle cerebellar peduncle.

THE BRAIN STEM

THE MEDULLA OBLONGATA. The brain stem in its oblongatal portion shows distinctive features along its ventral surface. The ventromedian sulcus is in relation upon either side with two elevations forming the pyramids which taper at their caudal extremities to a level where interlacing bundles of the decussation cross the sulcus. A well-defined preolivary sulcus separates the pyramid from a prominent olivary eminence, which latter is in turn separated from the spinocerebellar eminence by the postolivary sulcus. An intermediate sulcus indicates the boundary between this latter eminence and the eminentia trigemini. Upon the dorsal surface both the cuneus and the clava are prominent and separated from each other by the dorsal paramedian sulcus. As to relative volume, the ratio of the clava to the cuneus is about one to two, thus indicating from surface markings at least a preponderance of incoming sensory impulses from the upper extremity and hand. This accords with the failure on the part of the animal to develop a tail and also with the progress which it has made in its manual differentiation.

The dorsal aspect of the oblongata comprises its two characteristic surfaces, the infraventricular and the ventricular. The ventricular surface presents the lower angle of the fourth ventricle whose floor is bounded by the elevations formed by the cuneus and the clava. The floor contains the usual markings indicating the trigonum hypoglossi and the fovea vagi. As the lateral recesses are approached the two elevations formed by the clava and cuneus decrease in height and finally attain the level of the floor itself. At this point the entering fibers constituting the striae acusticae cross the floor toward the midline, most of them with an obliquity downward and inward. As they enter the ventricular cavity these fibers either cross or become submerged within an elevation situated near the lateral recess. This elevation is the vestibular eminence. In the orang its prominence in the floor of the ventricle is relatively less pronounced than in the lower and intermediate primates, but somewhat more conspicuous than in the chimpanzee, gorilla and man. A median sulcus symmetrically divides the floor of the ventricle into two longitudinal halves. The upper angle of the ventricular chamber is contained in the metencephalic portion of the stem. Above the striae acusticae a slight elevation marks the position of the nucleus abducentis. In other particulars the markings upon the ventricular floor are rather indefinite. The lateral walls of this portion of the ventricle are formed by the converging superior cerebellar peduncles. The ventricular cavity itself becomes more attenuated as the caudal orifice of the Sylvian aqueduct is approached.

The Pons Varolii. Upon the ventral surface at the cephalic extremity of the oblongata a marked bulbopontile sulcus draws the line of demarcation between the bulb and the pons Varolii. The latter structure is fairly large and prominent. Standing out conspicuously in the base of the brain, it is indicative of an animal possessed of a considerable connection between the cerebral hemispheres and the lateral lobes of the cerebellum. The inference permissible from such an ample pallio-cerebellar communication is that the motor organization of orang represents a relatively wide range of skilled performances, while the neokinetic acquisitions of the animal ally it to that group of the primates standing at or near the summit of this order.

The cephalic boundary of the pons is indicated by the pontopeduncular

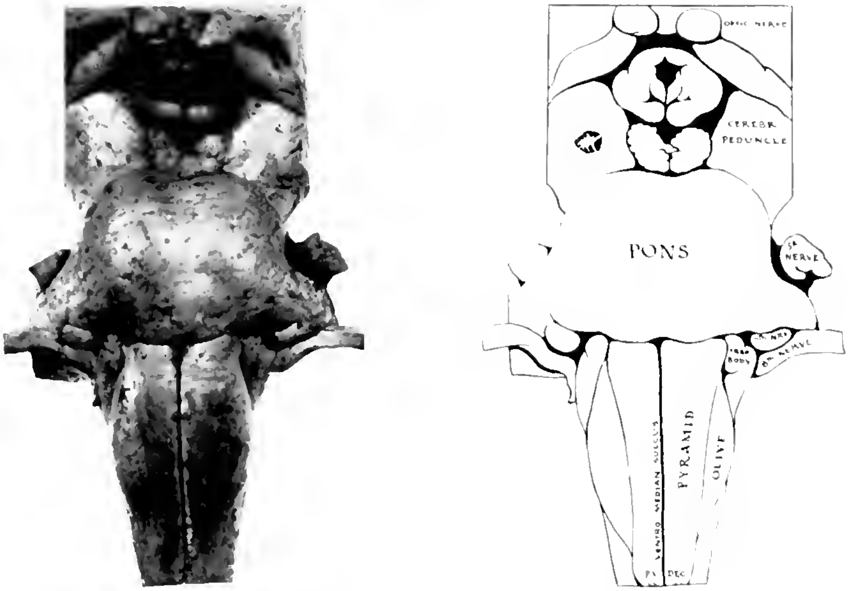


FIG. 227. VENTRAL SURFACE OF BRAIN STEM OF ORANG-OUTANG.
[Actual Length 54 mm.]

KEY TO DIAGRAM. CEREBR. PEDUNCLE, Cerebral Peduncle; PY. DEC., Pyramidal Decussation; TRAP. BODY, Trapezoid Body; 7TH NRV, Seventh Nerve.

sulcus which marks the beginning of the optico-peduncular space. The latter is bounded caudally by the divergent cerebral peduncles and cephalically by the optic chiasm and optic tracts. This space is prominent in the orang's brain, due to the conspicuous size of the two cerebral peduncles. The dorsal surface of the midbrain contains the usual specialization of the quadrigeminal plates giving rise to the superior and inferior colliculi. Of these the superior colliculus is somewhat more extensive, although having a less well-marked surface elevation. While the diameters of the inferior colliculus are less than those of the superior colliculus, its elevation is somewhat greater. The general deflorescence in these two specializations of the quadrigeminal plate in the orang indicates what is even more evident in cross section, i.e., a certain degree of involution incident to a delegation of the functions of hearing and vision

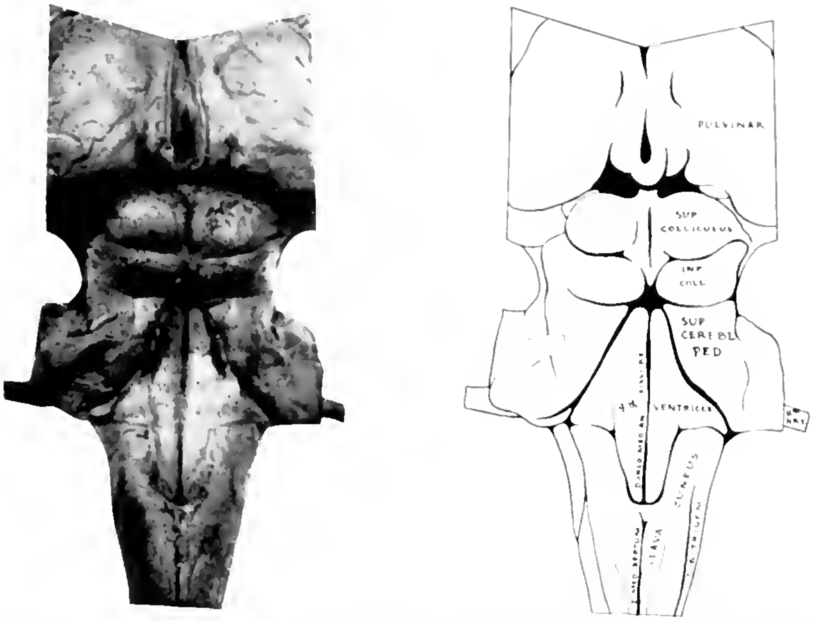


FIG. 228. DORSAL SURFACE OF BRAIN STEM, ORANG-OUTANG.
(Actual Length 54 mm.)

KEY TO DIAGRAM. D. MED. SEPTUM, Dorsomedian Septum; INF. COLL., Inferior Colliculus; SUP. CEREBL. PED., Superior Cerebellar Peduncle; SUP. COLLICULUS, Superior Colliculus; TUB. TRIGEM., Tuberculum Trigemini; 8TH NRV, Eighth Nerve.

to specialized areas in the cerebral hemisphere. Upon the lateral surface of the midbrain, a small elevation indicates the position of the mesial geniculate body, a relay station in the pathway of auditory sensibility.

INTERNAL STRUCTURE OF THE BRAIN STEM IN THE ORANG-OUTANG

The levels selected in the orang-outang correspond closely to those of the species already described. Any differences in the appearance of the several levels is met by the addition of supplementary sections including features which may not have appeared in the representative levels selected for description.

LEVEL OF THE PYRAMIDAL DECUSSATION (FIG. 229)

At the level of the pyramidal decussation the crossing fibers of the corticospinal tract make their usual impressive alterations. In consequence

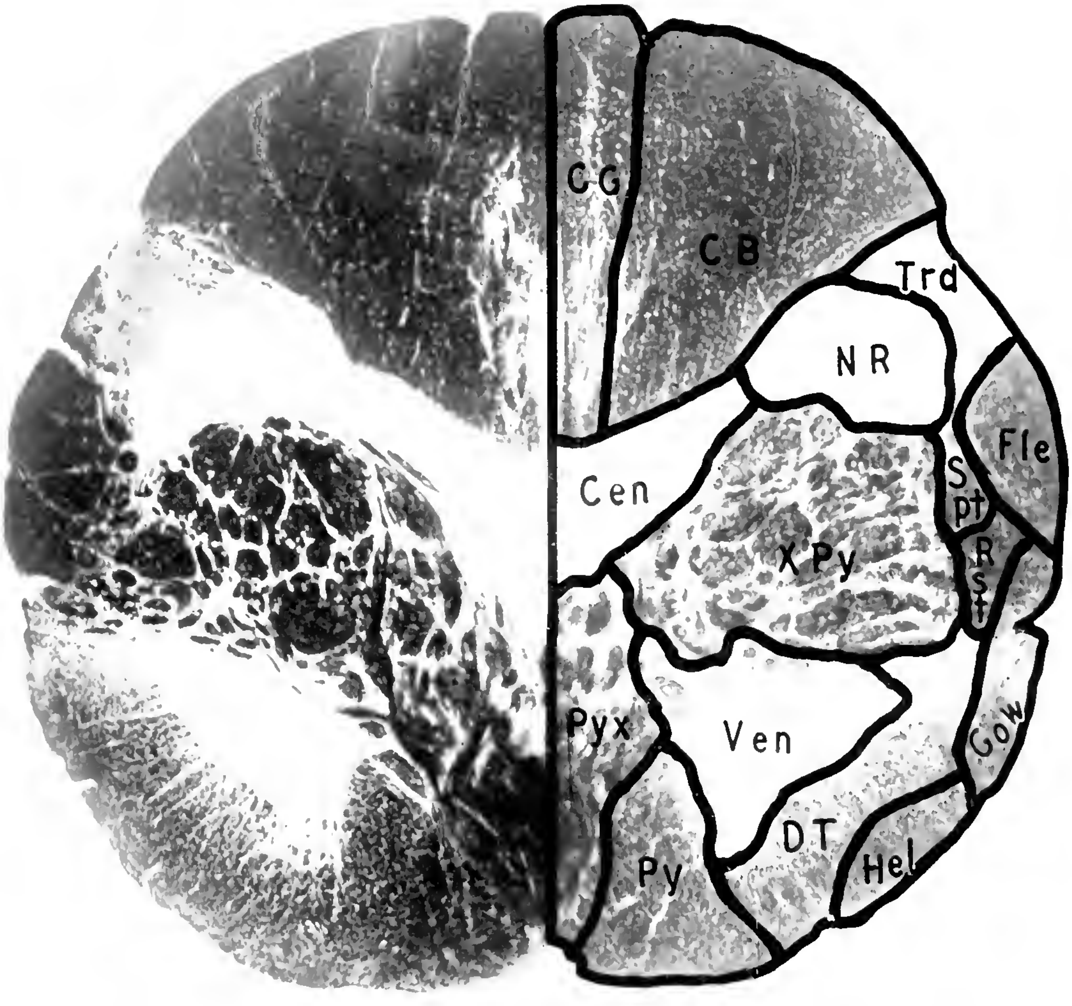


FIG. 229. ORANG-OUTANG. LEVEL OF THE PYRAMIDAL DECUSSATION.

CB, Column of Burdach; CEN, Central Gray Matter; CG, Column of Goll; DT, Deiterso-spinal Tract; FLE, Dorsal Spinocerebellar Tract; GOW, Ventral Spinocerebellar Tract; HEL, Spino-olivary Tract of Helweg; NR, Nucleus of Rolando; PY, Pyramid; PYX, Pyramidal Decussation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; TRD, Descending Trigeminal Tract; VEN, Ventral Gray Column; XPY, Crossed Pyramidal Tract. Accession No. 199. Section 55. Actual Size 12 × 11 mm.]

of the decussation (Pyx) the ventromesial sulcus is deflected to the left and the ventral gray column (Vcn) is almost entirely separated from the central gray matter (Cen). The latter structure has moved into a more caudal position in the early stages of that migration which eventuates in forming the floor of the fourth ventricle. In the most ventral portion of the section some fibers of the pyramid (Py) still keep their position characteristic of the oblongata. The dorsal sensory field is broad and expansive. It contains the usual elements: the column of Goll (CG) representing the leg, the column of Burdach (CB) representing the upper extremity, and the descending trigeminal tract (Trd) representing the sensory territories of the face. A small detached nuclear mass in the column of Goll represents the nucleus of Goll. No such nuclear structure is present in the column of Burdach. The nucleus of Rolando (NR), on the other hand, is of considerable size, although distinctly less in dimensions than is true of the lower or intermediate primates. The central gray matter (Cen) extends almost transversely across the section from a small central canal outward to the nucleus of Rolando. Immediately ventral to it are some of the collected bundles of the pyramid (XPy) in their course extending into the spinal cord. On the periphery of the section are the two spinocerebellar tracts (Fle, Gow), and ventromesial to the latter is the spino-olivary bundle of Helweg (Hel). The Deiterso-spinal tracts (DT) lie ventral to the ventral gray column (Vcn), while the rubrospinal (Rst) and spinothalamic (Spt) bundles occupy their usual positions in the intermediate medullary substance.

The interpretation to be given to this level with reference to its major functional elements concerns the marked increase in the volume of the pyramidal decussation, indicative of accessions in the voluntary control which the animal possesses over the muscles, and the large size of the column of Burdach as compared with the similar sensory columns providing influx from the lower extremity and from the head. The disparity which largely favors the column of Burdach clearly indicates what considerable gain the upper extremity has made as a discriminative and locomotor organ, and thus illustrates the reflection of that process which has as its ultimate goal the most complete differentiation of the upper extremity adapted to the purposes of neokinesis. The hand and the arm of the orang have not attained that degree of adaptability which is seen in either of the two other great anthropoids, the chimpanzee and the gorilla. On the other hand, as an organ for exploring the environment and for the production of many more complex and learned performances, the forelimb of the orang has made decisive advances over that of the gibbon or any of the intermediate primates.

LEVEL OF CAUDAL EXTREMITY OF DORSAL SENSORY NUCLEI (FIG. 230)

At this level the most important modifications have occurred in the dorsal fields where a detached nuclear mass near the dorsomedian septum has made its appearance. This is the nucleus of Goll (N G) which is invested by a dense mass of myelinized nerve fibers, the column of Goll (C G). The boundary line between this column and that of the column of Burdach (C B) is indicated by the presence of a poorly defined dorsal paramedian sulcus, while the lateral boundary of Burdach's column is nearly five times that of Goll. This coincides with the specialization going forward in the upper extremity of the animal, particularly the development of the hand and the long powerful forearm, while the absence of the tail and the relatively low degree of development in the short legs account for a difference in which the column of Goll appears to be the smaller of the two. No detached nuclear mass is seen as yet in the column of Burdach. Near the base of the central gray matter (Cen) a small dorsal protrusion marks the beginning of the caudal extremity of the nucleus of Burdach. These two nuclei in the dorsal column present, throughout the entire series of primates, a contrasting feature which may be mentioned here: The caudal extremity of the nucleus of Goll invariably has no direct connection with the central gray matter; such connection as it does ultimately attain is tenuous and reticular

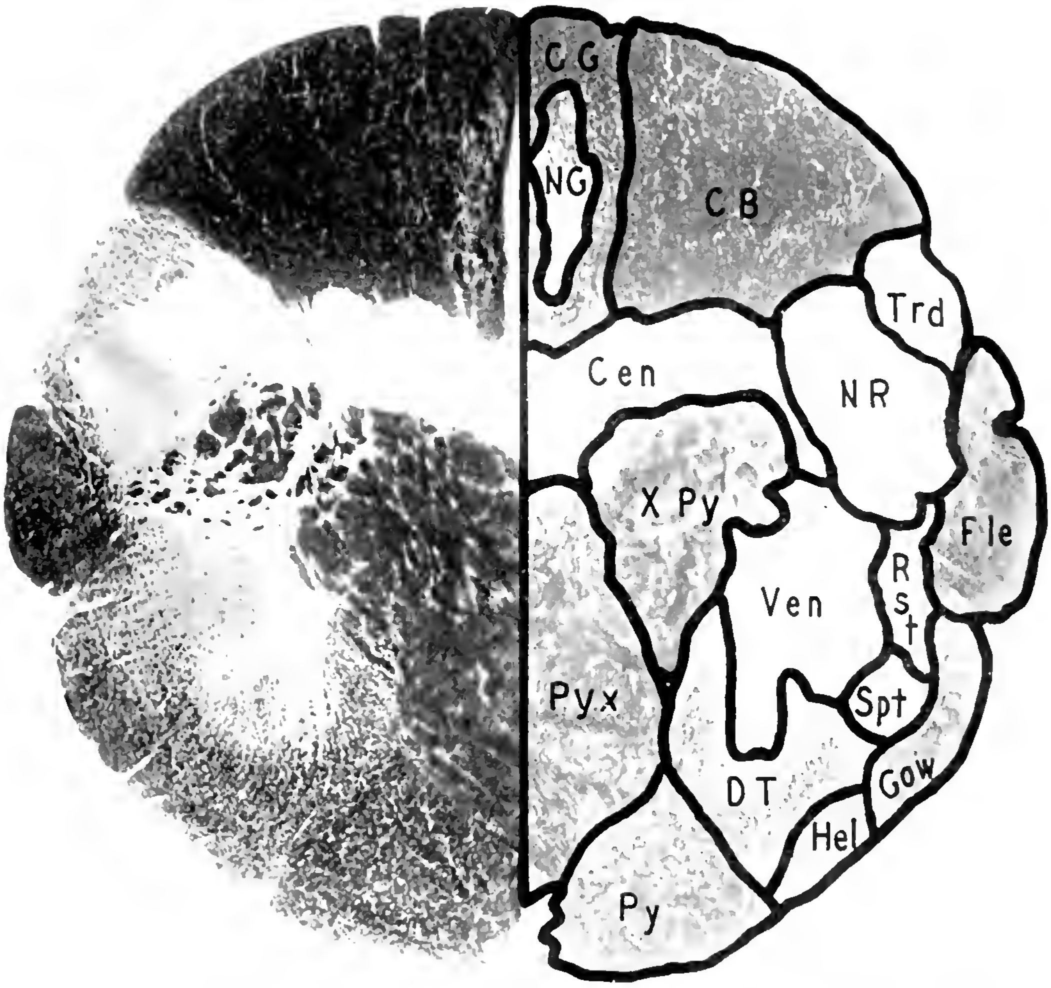


FIG. 230. ORANG-OUTANG. LEVEL OF THE CAUDAL EXTREMITY OF THE DORSAL SENSORY NUCLEI.

CB, Column of Burdach; CEN, Central Gray Matter; CG, Column of Goll; DT, Deiterso-spinal Tract; FLE, Dorsal Spinocerebellar Tract; GOW, Ventral Spinocerebellar Tract; HEL, Spino-olivary Tract of Helweg; NG, Nucleus of Goll; NR, Nucleus of Rolando; PY, Pyramid; PYX, Pyramidal Decussation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; TRD, Descending Trigeminal Tract; VEN, Ventral Gray Column; XPY, Crossed Pyramidal Tract. Accession No. 100. Section 95. Actual Size 14 × 12 mm.

in form. The nucleus of Burdach in its caudal extremity, on the other hand, appears as a definite extension from a dorsal prolongation of the central gray matter. It presents no detached prolongation into the surrounding medullary substance. Its structural connection with the central gray matter is much more decisive and appears in the form of a compact, discretely circumscribed dorsal projection in this region. In this sense it has much the same appearance of continuity in the gray matter as there is in the nucleus of Rolando (substantia gelatinosa trigemini) (N R). In connection with the nucleus of Goll there is no unpaired median nucleus of Bischoff, which fact again supports the idea that this median nucleus develops in connection with the tail.

The central gray matter (C e n) is elongated laterally and stretches as a narrow band along the ventral border of the dorsal sensory fields. It contains at its center a small central canal, and extends laterally to become continuous with the expanding dorsal horn now presenting itself in the form of the substantia gelatinosa trigemini (N R) (the nucleus of Rolando). This nucleus is in contact by its lateral margin with a collection of fibers constituting the descending trigeminal tract (T r d). Ventral to the central gray matter are the decussating fibers of the pyramid (P y x) which have the appearance of compact bundles closely interlacing as they cross from one side to the other. Their decussation separates the ventral gray column (V e n) from the central gray (C e n). The separation at this level is not quite complete as there still remain a few strands or bridges of gray matter connecting the central gray with the ventral gray column. Some idea of the massiveness of the pyramidal decussation may be obtained in this section. The mass of fibers affords an opportunity for estimating the volume of impulses necessary to the volitional control of the muscles. Ventral to the substantia gelatinosa and on the periphery of the axis is a dense collection of fibers which produce a surface prominence, the spinocerebellar eminence separated from the eminentia trigemini by the sulcus intermedius. The spinocerebellar eminence contains ascending fibers from the proprioceptive system destined for the cerebellum, and comprising the dorsal spinocerebellar tract. This eminence is a well-defined feature of the brain stem of the primates, but becomes especially demarcated as a surface feature in the anthropoids and man. Its progressive distinction through the higher anthropoids, until it reaches its most clearly defined demarcation in man, gives further evidence of that process which results in the sharper definition of all brain stem structures in ascending the primate series.

Lateral to the external limit of the pyramid on the circumference is a small groove which indicates the caudal extremity of the preolivary sulcus. Further along the periphery is the caudal extremity of the post-olivary sulcus. The eminence which is thus demarcated, although of slight prominence, occupies the position at which the inferior olivary nucleus appears in higher levels, in consequence of whose appearance the olivary eminence is determined.

At this level the more or less detached ventral gray column is contained within the limits indicated by the beginning of the two olivary sulci. On the outer margin of the ventral gray column, ventrolateral to the central gray column, are the descending Deiterso-spinal tract (DT), the rubrospinal (Rst) and spinothalamic (Spt) tracts. Upon the actual periphery of the circumferential zone are the fibers constituting the ventral spinocerebellar tract (Gow).

This section indicates accessions to the animal's sensory sphere, especially in the field of discriminative sensibility. It also points to a lesser degree of sensory influx from the lower extremity. The extent of volitional control inherent in this animal is indicated by the volume of the pyramidal decussation (Pyx). The tendency of the central gray matter to move into a dorsal position in the cross section is shown as a step preparatory to the ventriculation which occurs in the higher levels of the oblongata.

LEVEL OF THE CAUDAL EXTREMITY OF THE INFERIOR OLIVE (FIG. 231)

At this level the principal addition is a small mass of gray matter constituting the caudal tip of the inferior olivary nucleus (IO) situated

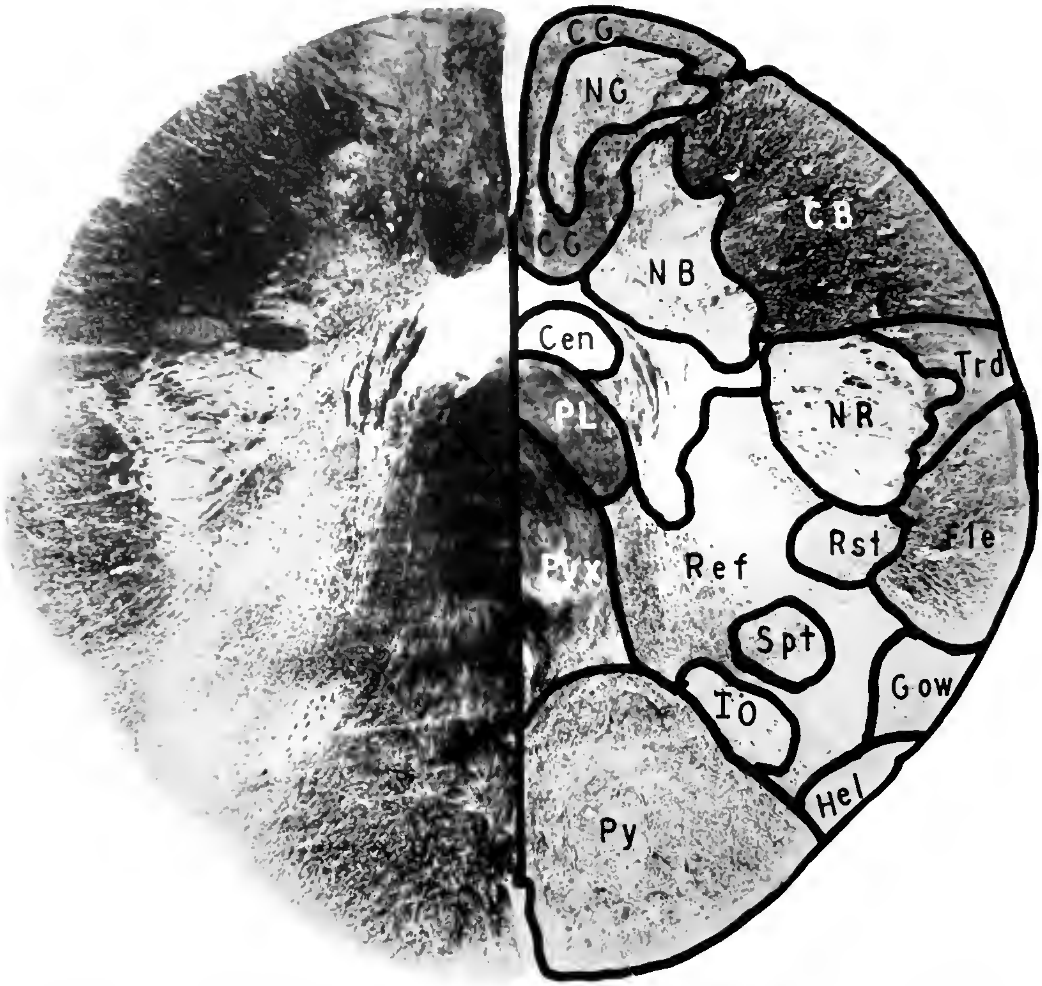


FIG. 231. ORANG-OUTANG. LEVEL OF THE CAUDAL EXTREMITY OF THE INFERIOR OLIVE.

CB, Column of Burdach; CEN, Central Gray Matter; CG, Column of Goll; TIT, Dorsal Spinocerebellar Tract; GOW, Ventral Spinocerebellar Tract; HEL, Spino-olivary Tract of Helweg; IO, Inferior Olive; NB, Nucleus of Burdach; NG, Nucleus of Goll; NR, Nucleus of Rolando; PL, Posterior Longitudinal Fasciculus; PY, Pyramid; PYX, Pyramidal Decussation; REF, Reticular Formation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; TRD, Descending Trigeminal Tract. [Accession No. 100. Section 60. Actual Size 12 × 11 mm.]

dorsolateral to the pyramid (Py), some of whose fibers are still in process of decussation (Pyx). The entire section has increased in its diameters, largely due to the expansion occasioned by the increment in the dorsal sensory nuclei, the addition of the inferior olivary nucleus and the introduction of decussating fibers from the nucleus of Goll. These internal arcuate fibers pass ventrad to the central gray matter (Cen) into the median raphe where they undergo decussation, and enter the mesial fillet. The central gray matter (Cen), somewhat irregularly quadrilateral in outline, is partially detached from connection with the remaining gray matter by the internal arcuate fibers. It has migrated dorsad, with the effect that the dorsomedian septum is beginning to expand and cause the divergence of the opposed surfaces of the two alar plates. In the center of the gray matter is a small central canal. The dorsal sensory fields are occupied by the much increased nuclei of Goll and Burdach (NG, NB), to the latter of which are appended scattered nuclear masses forming the nucleus of Blumenau. The relative proportions of the nuclei of Goll and Burdach are clearly indicated by the dorsal paramedian sulcus. The substantia gelatinosa trigemini (NR) occupies its usual position lateral to the nucleus of Burdach. It is of considerable size and accompanied by a large descending trigeminal tract (Trd). Ventral to the substantia gelatinosa is the gray matter constituting the griseal portion of the reticular formation (Ref). Its indefinite and diffuse character is conspicuous at this level. This portion of the central axis in the orang contains much of this ill-defined differentiation which is more characteristic of the lower and intermediate primates than it is of the great anthropoids.

The ventromesial area of the cross section is occupied by the pyramid (Py), some fibers of which are still undergoing decussation in a position ventral to the accumulating fibers forming the mesial fillet. Lateral to the pyramid is the preolivary sulcus and, somewhat further along the periphery of the section, a faint indenture marks the postolivary sulcus.

The impression created by this level of the brain stem makes more clear the accessions in the dorsal sensory field which particularly affect the column of Burdach. This appears to be related to the differentiation of the forearm and hand. The substantia gelatinosa is relatively small, indicating a less voluminous sensory contribution from the head and face than is the case in many of the lower primates.

LEVEL THROUGH THE MIDDLE OF THE INFERIOR OLIVE (FIG. 232)

Here the large mass of gray matter occupying the ventrolateral portion of the field constitutes the most prominent feature. This is the inferior olivary nucleus (IO) which in the orang-outang calls for special comment. In the first place, the size of the structure in proportion to the rest of the cross section has obviously increased, thus indicating that the olivary functions have proportionately advanced in their importance to the animal. In addition, there is distinct progress in the degree of convolution or festooning presented by the saccular wall of the nucleus, a feature which is more particularly in evidence along the dorsolateral and ventromesial portion than in the olivary fundus. A third feature is the somewhat clearer definition of the nucleus as a whole, in contrast with adjacent structures. In this respect, however, the degree of definition marking the boundaries of the inferior olive in the orang is less decisive than in chimpanzee, in gorilla or in man.

In view of the function ascribed to the inferior olivary nucleus in this discussion, it would appear that the orang is endowed with a greater degree of coordination between head, hand and eye and of coordination of all skilled learned performances than is the case in the lower primates. This is also true to some extent in the comparison with the intermediate primates.

When contrasted with the higher members of this order, the morphological evidence in orang indicates an animal less highly organized in this respect. The motor performances of orang, in part at least, bear out this supposi-

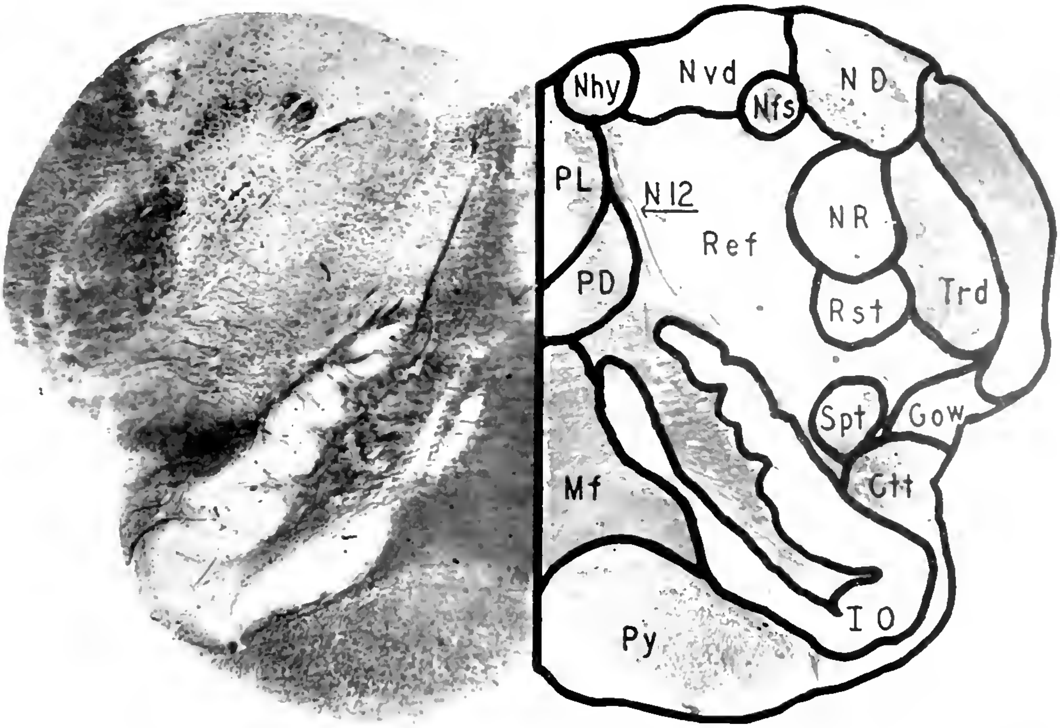


FIG. 232. ORANG-OUTANG. LEVEL THROUGH MIDDLE OF INFERIOR OLIVE.

CTT, Central Tegmental Tract; TTT, Dorsal Spinocerebellar Tract; GOW, Ventral Spinocerebellar Tract; IO, Inferior Olive; MF, Mesial Fillet; ND, Deiters' Nucleus; NTS, Nucleus Solitarius; NHY, Hypoglossal Nucleus; NR, Nucleus of Rolando; NVD, Dorsal Vagal Nucleus; N12, Hypoglossal Nerve; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PY, Pyramid; REF, Reticular Formation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; TRD, Descending Trigeminal Tract. [Accession No. 100. Section 245. Actual Size 18 × 11 mm.]

tion. The mode of its life does not require so high a degree of specialization in the forelimbs as that of the chimpanzee, of the gorilla or of man. Yet because the animal does assume a more or less upright position, especially when making its way along the branches of the trees, the forelimb has been emancipated in some measure, and the hand is thus freed for purposes of exploration and prehension in functional activities not directly connected with locomotion. Such specialization implies a greater need of intimate cooperation between the eye, neck and appendicular muscles of the forelimb.

This section, being somewhat higher than the corresponding levels of the forms previously illustrated, shows a slightly different arrangement of the structures bordering on the floor of the fourth ventricle. The ventricular floor is formed by the central gray matter in whose most mesial portion is the nucleus hypoglossus (N hy). The nucleus is somewhat more clearly delimited than in the lower primates, although it has by no means the sharp demarcation seen in the higher members of the order. The fibers of the twelfth nerve (N12) pass forward from the nucleus in the direction of the inferior olivary body. The nucleus is separated from an adjacent aggregation of gray matter by a definite groove, the sulcus limitans. This sulcus marks the position of the dorsal nucleus of the vagus nerve (N vd). At the lateral border of this vagal nucleus is an oval collection of myelinized axons forming the fasciculus solitarius which is surrounded by a special nuclear collection, the nucleus of the fasciculus solitarius (N fs). The caudal extremity of Deiters' nucleus (ND) occupies a lateral position beneath the floor of the ventricle. Ventral to this nucleus is the substantia gelatinosa (NR) whose outer margin is in contact with a large collection of fibers constituting the descending trigeminal tract (Trd). On the dorsolateral aspect of the section is the compact bundle of fibers forming the corpus restiforme (Fle) whose extension cephalad as the inferior cerebellar peduncle serves to form the ultimate connection of the lower segmental levels with the cerebellum. The reticular formation (Ref) is extensive but presents no specialized nuclear aggregations at this level. Occupying its characteristic ventromesial position, the pyramid (Py) forms a fasciculus of considerable size which, however, seems inferior in volume to this structure in the still higher primates. This bundle gives the impression that the orang is an animal less extensively provided with voluntary control over the somatic musculature than its higher congeners. Dorsal to the pyramid are the compact bundles constituting the mesial fillet (M f) paralleling which the fibers of the twelfth nerve pass forward, many of them to penetrate the inferior olivary body.

LEVEL OF THE VESTIBULAR NUCLEI (FIG. 233)

At the level of the vestibular nuclei, which is somewhat higher than the corresponding sections in the other forms, the principal feature appears in the nuclear complex related to the balancing mechanism, as it receives fibers from the utricle, saccule and semicircular canals. This complex is composed of the vestibular nuclei. The nucleus of Schwalbe (N Sc) lies in intimate relation with the floor of the fourth ventricle. It has its usual triangular outline, but is less well defined than the structures lateral to it. The nucleus of Deiters (N D) is typical in its appearance, consisting of nuclear substance dispersed throughout which are numerous small bundles of myelinized axons. Lateral to Deiters' nucleus is the corpus restiforme (ICP) which passes cephalad as the inferior cerebellar peduncle. Bordering upon its lateral surface is the mass of gray matter constituting the tuberculum acusticum (Tub), connected with the cochlear division of the eighth nerve (N 8), the fibers of which penetrate this eminence. Ventral to Deiters' nucleus is the substantia gelatinosa (N R) surrounded on its outer surface by the compact bundles forming the descending trigeminal tract (Trd). Entrant root fibers of the vestibular division of the eighth nerve pass either through the substantia gelatinosa or between it and the corpus restiforme on their way to Deiters' nucleus. The prominence of the vestibular area as it appears in relief in the floor of the fourth ventricle, as well as the dimensions of these two nuclear structures seen in cross section, convey the impression of a balancing mechanism upon which less demand is made than in the lower, more strictly arboreal primates. The orang is altogether slower in its locomotion, both in its arboreal pursuits and on those

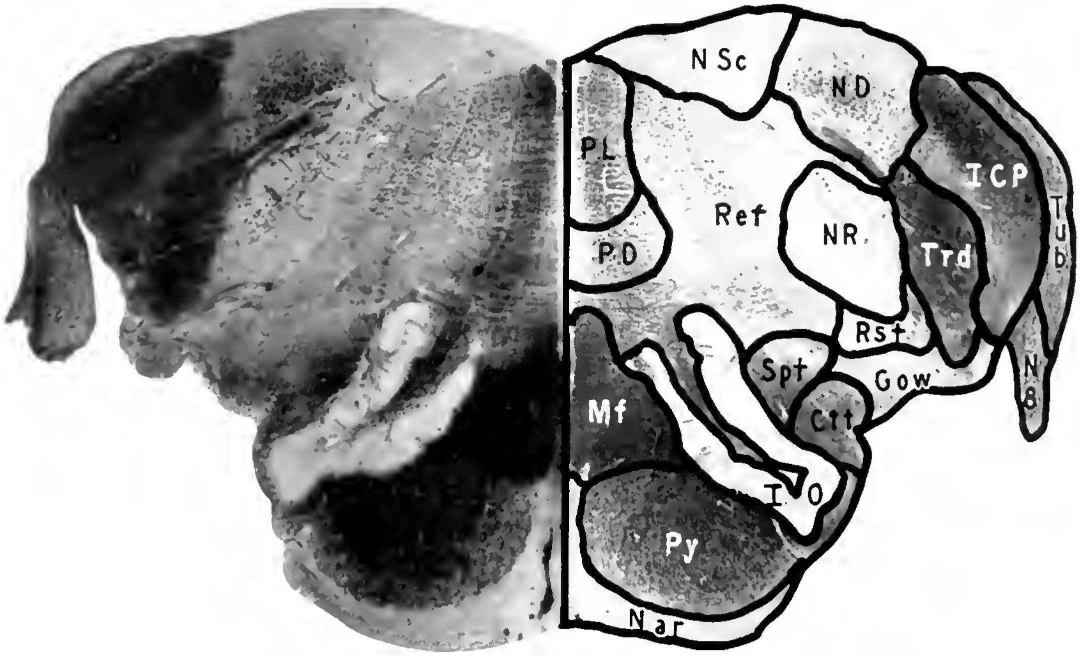


FIG. 233. ORANG-OUTANG. LEVEL OF THE VESTIBULAR NUCLEI.

CTT, Central Tegmental Tract; GOW, Ventral Spinocerebellar Tract; ICP, Inferior Cerebellar Peduncle; IO, Inferior Olive; MF, Mesial Fillet; NAR, Nucleus Arciformis; ND, Deiters' Nucleus; NR, Nucleus of Rolando: NSC, Nucleus of Schwalbe; N8, Acoustic Nerve; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PY, Pyramid; RET, Reticular Formation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; TRD, Descending Trigeminal Tract; TUB, Tuberculum Acusticum. [Accession No. 100. Section 285. Actual Size 20 × 12 mm.]

rarer occasions when it goes upon the ground. The difference in all probability is slight, for the efficacy of the balancing mechanism seems to be fairly well standardized. What one species requires most in some specialized direction is less essential to other forms. An averaging of balancing requirements seems to equalize the development of equilibratory structures.

In the ventrolateral portion of the section, the cephalic extremity of the inferior olive appears (IO), and mesial to it the bundles constituting the pyramid (Py). Extending directly backward toward the floor of the ventricle is the dense bundle of the mesial fillet (M f). Ventromesial to the pyramid is a large collection of gray matter constituting the arciform nucleus (Nar) which, in all probability, is a caudal extension of the pontile nuclei. In any case, these two nuclear structures are definitely continuous, thus creating the impression that expansions of the nuclear specializations of the pons have resorted to a caudal extension in order to accommodate their apparently exuberant growth.

LEVEL OF THE CEREBELLAR NUCLEI (FIG. 234)

At the level of the cerebellar nuclei the contour of the section has undergone marked alteration chiefly because of the continuity of the stem with the cerebellum by means of the middle cerebellar peduncle (Mcp). The large mass of the medullary vestibule of the cerebellum appears on the lateral aspect of the section and contains the somewhat convoluted and poorly defined nucleus dentatus (Ndt). Mesial to it in the roof of the ventricle is the nucleus globosus. Both the size and definition of the dentate nucleus, as compared with the lower primates, indicate an animal with a greater degree of coordinative control over the musculature. Although the increased dimensions of the dentate nucleus as compared with the lower primates is evident, there is an equally striking contrast when this nucleus is compared with that of the higher forms. It then appears less well defined, less prominent and smaller than in the other great anthropoids, implying that orang is not so well provided in muscular coordination as those primates standing above it in the scale.

The central gray matter forms the floor of the ventricle (Ven IV) without special nuclear differentiation. Mesially, the posterior longitudinal fasciculus comes closer to the ventricular floor than is the case at lower levels. Some fibers of the cochlear division of the eighth nerve (N 8) enter the dorsal cochlear nucleus, and others, either as secondary relay fibers or as fibers primarily received from the cochlear division itself, pass inward and forward along the ventral portion of the tegmentum to form the massive

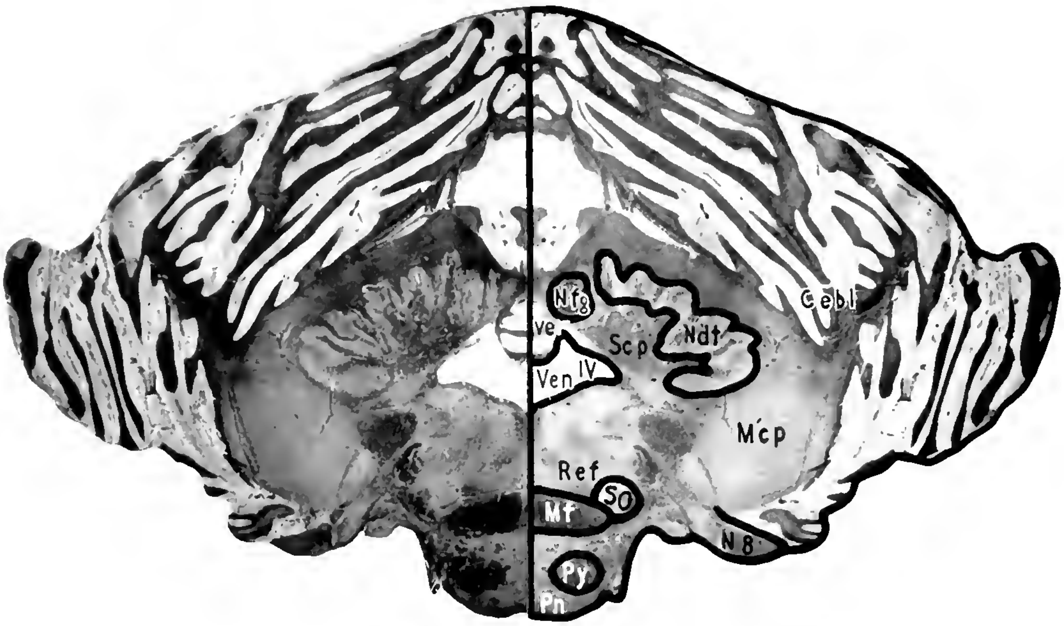


FIG. 234. ORANG-OUTANG. LEVEL OF THE CEREBELLAR NUCLEI.

CEBL, Cerebellum; MCP, Middle Cerebellar Peduncle; MF, Mesial Fillet; NDT, Cerebellar Nuclei, Lateral Group; NFG, Cerebellar Nuclei, Mesial Group; N8, Auditory Nerve; PN, Pontile Nuclei; PY, Pyramid; REF, Reticular Formation; SCP, Superior Cerebellar Peduncle; SO, Superior Olive; VEN IV, Fourth Ventricle; VER, Vermis Cerebelli. [Accession No. 100. Section 365. Actual Size 45 × 25 mm.]

decussation of the corpus trapezoideum. At the lateral extremity of the corpus trapezoideum is an aggregation of gray matter, the caudal extremity of the superior olivary nucleus (SO). This nucleus, like the trapezoid body, is related to the conduction of auditory impulses received by the cochlear division of the eighth nerve. Ventrolateral to the entering fibers of the cochlear division of the eighth nerve is the substantia gelatinosa Rolandi surrounded upon its lateral aspect by the descending trigeminal tract. Directly ventral to the substantia gelatinosa is a well-defined nuclear mass, the nucleus facialis. From this facial nucleus many myelinized fibers pass backward and inward, toward the floor of the fourth ventricle where they become assembled to form the second portion of the emergent course of the seventh nerve. In their usual ventral area are the fibers constituting the pyramid (Py), now surrounded by a large nuclear aggregation, the caudal extremity of the pontile nuclei (PN). Lying in a position more transverse than in the lower sections, is a bundle of fibers marking the boundary between the tegmentum and the basis, the mesial fillet (Mf), through which pass the decussating fibers of the corpus trapezoideum. Thus at this level it is possible to make a fairly accurate comparison of the volume of impulses passing over the mesial fillet and the pyramid. Both of these fasciculi appear more ample than in the lower primates, a conclusion which would justify the impression that orang is an animal more highly endowed in discriminative sensibility and also in volitional control of motion.

LEVEL NEAR THE CAUDAL LIMIT OF THE PONS VAROLII SHOWING THE EMERGENT FIBERS OF THE SIXTH NERVE (FIG. 235)

Here the section presents those marked changes incident to the appearance of the typical pontile stratification. The pons consists of the stratum superficiale; the stratum complexum, containing the large mass of pontile nuclei, transverse fibers and the scattered bundles of the pyramidal system, and the stratum profundum composed largely of transverse fibers. The general size of the pons Varolii, especially of the pontile nuclei, implies an animal possessed of a high degree of coordinative control over the more complex acquired movements. It indicates an ample communication between several areas of the neopallium and the lateral lobes of the cerebellum. The pallio-ponto-cerebellar system, as has already been shown in previous discussions, is characteristic of the mammalian brain alone. Its predominant developmental feature is witnessed in the expansion of the cerebral hemispheres. The fact that this system, which connects the cerebral cortex with the cortex of the lateral lobes of the cerebellum, should manifest itself only in the mammal,

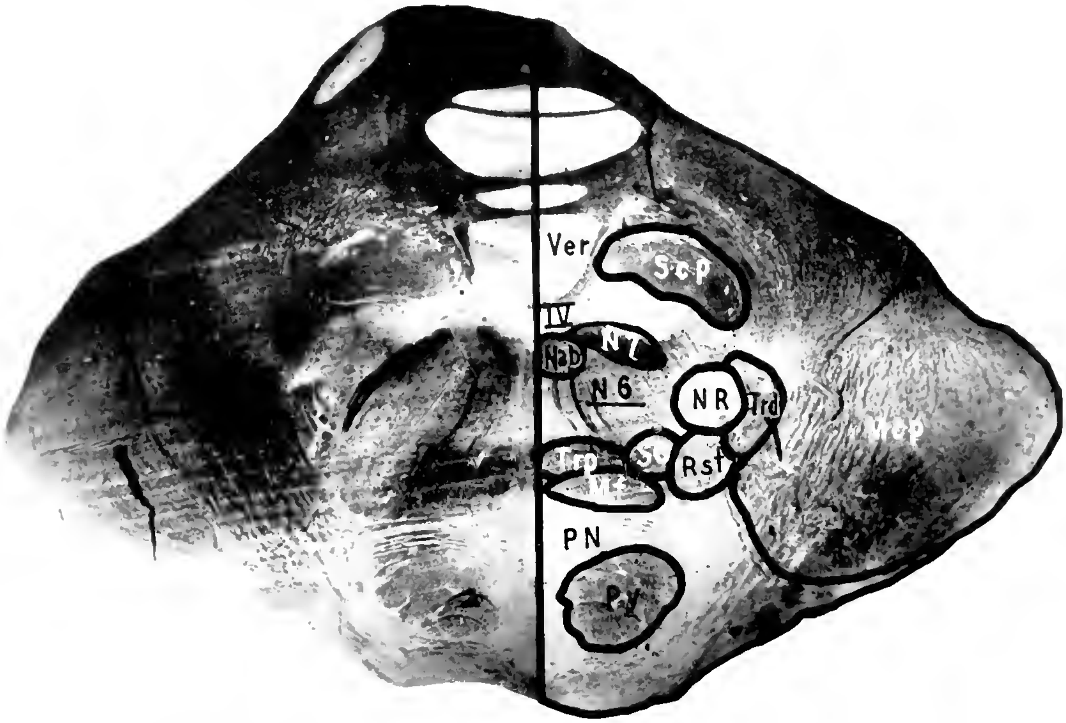


FIG. 235. ORANG-OUTANG. LEVEL NEAR THE CAUDAL LIMITS OF THE PONS, SHOWING THE EMERGENT FIBERS OF THE SIXTH NERVE.

MCP, Middle Cerebellar Peduncle; MF, Mesial Fillet; NAB, Abducens Nucleus; NR, Nucleus of Rolando; N6, Abducens Nerve; N7, Facial Nerve; PN, Pontile Nuclei; PY, Pyramid; RST, Rubrospinal Tract; SCP, Superior Cerebellar Peduncle; SO, Superior Olive; TRP, Trapezoid Body; TRD, Descending Trigeminal Tract; IV, Fourth Ventricle; VER, Cerebellar Vermis. [Accession No. 100. Section 410. Actual Size 40 × 25 mm.]

denotes the introduction into mammalian organization of a feature, which, if not morphologically new, is at least productive of new attainments. As such it calls for comparison with the inframammalian species to determine what decisive physiological accession to vertebrate behavior brought this important system into existence.

Many facts already exist to prove the essential relation of the lateral lobes of the cerebellum to the arms and the legs. Similar indications point to expansions in the neopallium as a response to this limb specialization. This evidence seems to put beyond peradventure the question that appendicular specialization supplies the developmental motive which underlies such far-reaching differentiation in the central nervous system. But limbs are almost as ancient as the vertebrate stock itself. They are not characteristic of the mammalian class alone. Some specialized element intrinsic to the extremities, and not necessarily apparent in their morphological structure, therefore, must be sought to explain this pronounced development of the mammalian hemispheres, cerebral as well as cerebellar. However convergent or divergent the fore- and hindlimbs of reptiles and birds, amphibia and fish may be in structural comparison with those of mammals, there is a functional divergence between them which is constant. In inframammalian orders all movements of the limbs tend to be synchronized with the movements of the body and with each other. There appears to be little need of independent motion on the part of one or the other limb.

In the mammals, on the other hand, there is an increasing degree of independent action in the fore- and hindlimbs and also in one forelimb independent of the other. Similarly, one hindlimb may act independently of all the others. Such independence of action strikes a new note in the motor organization of the extremities. The appendicular musculature liberated itself from that dominating dependency of interaction existing between the movable parts of the body. It gained a freedom which determined a new motor objective. Each limb, having acquired an individuality of its own, develops a specific sphere of action. In this sense the fore and hind extremities of mammals differ from those of lower vertebrates. Serving as more or less highly individualized instruments, the limbs are capable of expressing what amounts to a new physiological endowment. At the same time they retain many details of their primordial subjugation in that community of interests necessary to cooperation of the entire musculature for the purposes of locomotion. In their more recently acquired capacity, the extremities developed numerous performances, new both in design and range, which called for expansions in the controlling mechanisms of the central nervous system. The neopallium was the brain's structural response to this demand, simultaneously with which the cerebellum expanded to afford a needed increase of coordinative control for these new activities. It is evident that all of this motor adaptation belonged to what may be called *neokinetic organization*, which differs materially from those older, more primordial activities which are attributed to the *paleokinetic organization* of lower vertebrates. The pontile structures denoting this neokinetic expansion in the pallio-ponto-cerebellar system are evident in the orang; if not so prominent as in the higher anthropoids, they are still much more conspicuous than in the lower and intermediate primates.

The distinction between the basis pontis and tegmentum pontis is established by the transverse position of the mesial fillet (M f) which occupies the most ventral position in the tegmental portion of the stem at this level. The transverse fibers of the basis pontis are shown in their collected mass as they constitute the middle cerebellar peduncle (M cp). The central gray matter forms the floor of the fourth ventricle (IV) and is specialized in its median portion as a nucleus giving rise to the sixth cranial nerve (N ab). The fibers of this nerve (N 6) pass from the nucleus in the direction of the basis toward their point of emergence in the bulbopontile sulcus. Lateral to this nucleus is a dense bundle of emergent fibers constituting the fourth part of the intramedullary course of the facial nerve (N 7). Mesial to the bundles forming this emergent root is the caudal extremity of the nucleus facialis itself. The roof of the ventricle is formed by the inferior portion of the cerebellar vermis (Ver). The reticular formation embraces the most extensive portion of the tegmentum but shows no specialized nuclear collections at this level, nor are its boundaries well defined.

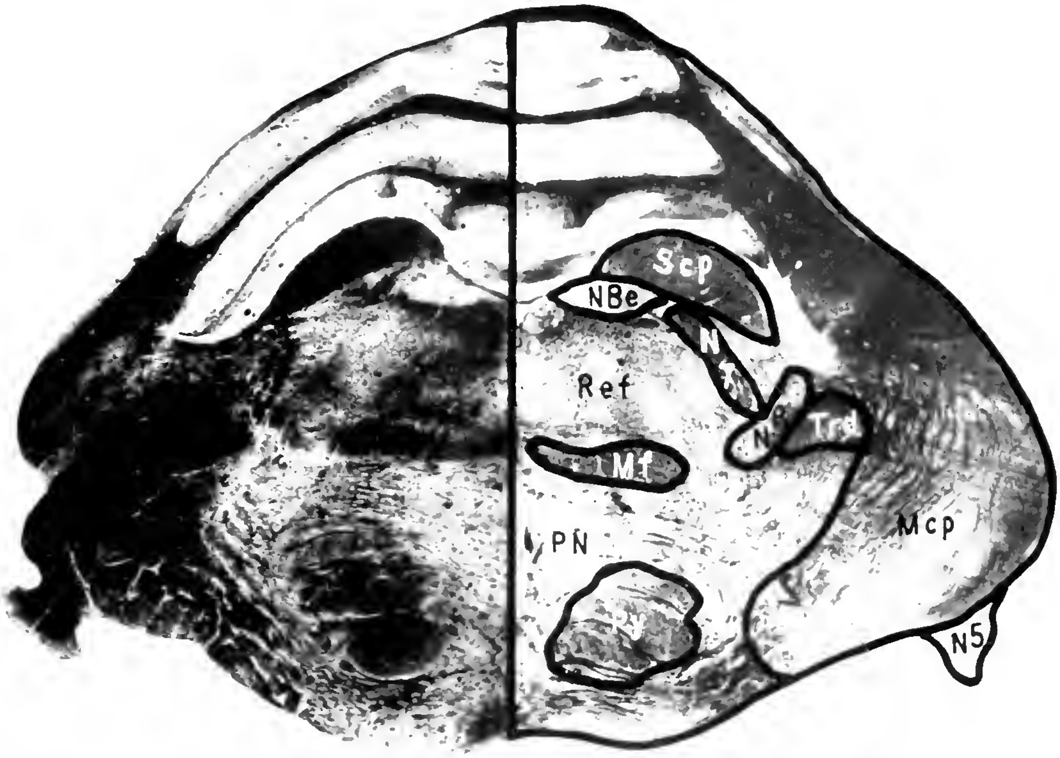


FIG. 236. ORANG-OUTANG. LEVEL OF THE MIDDLE OF THE PONS VAROLII. MCP, Middle Cerebellar Peduncle, MF, Mesial Fillet; NBE, Nucleus of Bechterew; NR, Nucleus of Rolando; N5, Trigeminal Nerve; N7, Facial Nerve; PN, Pontile Nuclei; PY, Pyramid; RET, Reticular Formation; SCP, Superior Cerebellar Peduncle; TRD, Descending Trigeminal Tract. [Accession No. 100. Section 460. Actual Size 28 × 10 mm.]

It gives the impression of a diffuse region of undifferentiated gray and white substance.

LEVEL THROUGH THE MIDDLE OF THE PONS VAROLII (FIG. 236)

Here the section shows all of the salient features in the stratified appearance of the pons Varolii. These include the stratum superficiale, the complexum and the profundum. They afford again an opportunity for estimating the relative size of the pontile nuclei (PN). The transverse fibers of the pons are collected to form the middle cerebellar peduncle (Mcp). The central

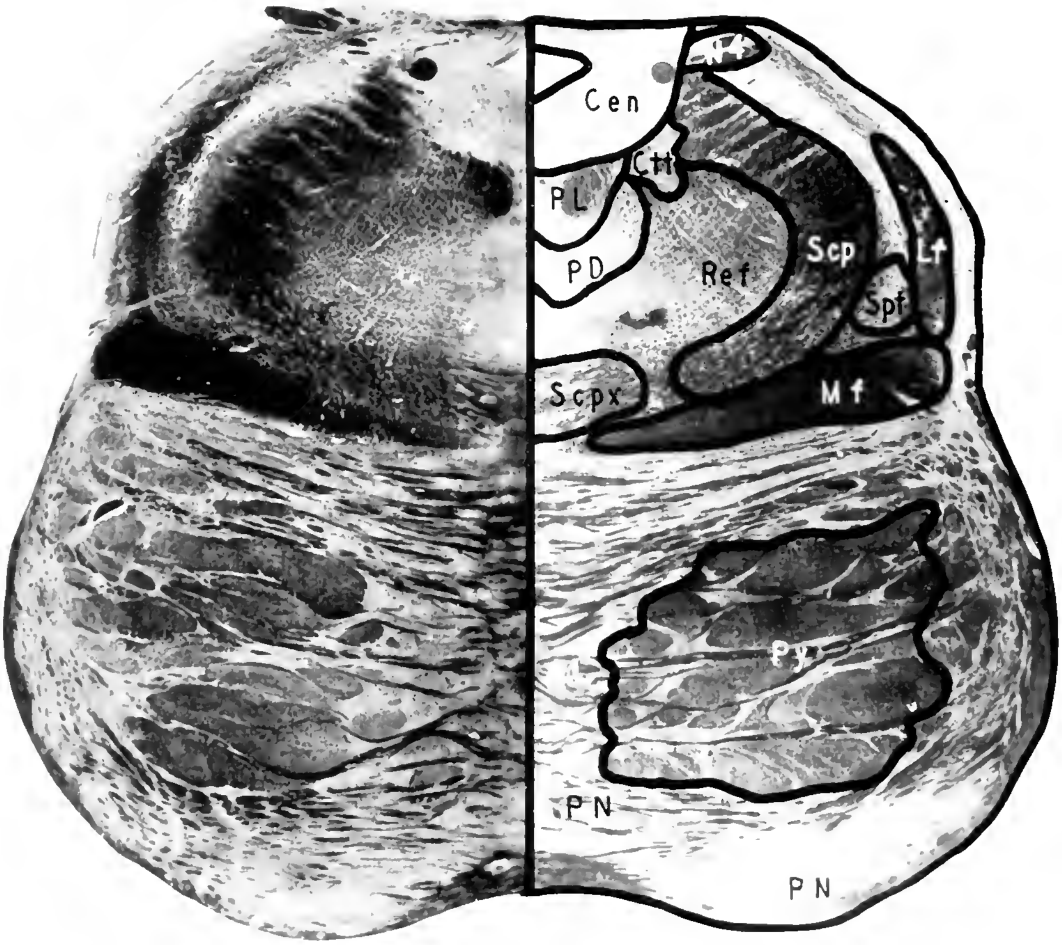


FIG. 237. ORANG-OUTANG. LEVEL OF EMERGENCE OF TROCHLEAR NERVE.

CEN, Central Gray Matter; CTT, Central Tegmental Tract; LF, Lateral Fillet; MF, Mesial Fillet; N4, Trochlear Nerve; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PN, Pontile Nuclei; PY, Pyramid; REF, Reticular Formation; SCP, Superior Cerebellar Peduncle; SCPX, Decussation of the Superior Cerebellar Peduncle; SPT, Spinothalamic Tract. [Accession No. 100. Section 560. Actual Size 10 × 16 mm.]

gray matter, while reduced in size, forms the floor of the ventricle whose general dimensions are now considerably less than in the lower levels, due to the fact that the ventricular chamber is approaching the caudal orifice of the Sylvian aqueduct. The floor of the ventricle shows no particular nuclear specialization. In it are the transverse fibers constituting the third portion of the facial nerve in its emergent course from the brain, known as the *genu facialis* (N 7). Entering in relation to the beginning of the middle cerebellar peduncle are the fibers of the dorsal root of the trigeminal nerve (N 5). These fibers pass inward to come into relation with a somewhat convoluted mass of gray matter, the cephalic extremity of the substantia gelatinosa trigemini, here forming the convolutiones quinti (NR), and ventral to it a large homogeneous nucleus from which arise the fibers forming the motor root of the trigeminal nerve, the nucleus masticatorius. The lateral walls of the fourth ventricle at this level are produced by the massive collection of fibers constituting the superior cerebellar peduncle (Scp).

LEVEL OF THE INFERIOR COLLICULUS (FIG. 238)

At this level the contour of the section is considerably modified by the appearance of two elevations in the roofplate of the midbrain. These are the inferior colliculi (IC) directly connected with the auditory system, since they serve as relay stations in that pathway. They were formerly of greater functional importance than in this or other primates. The ventral aspect of the section still retaining some of the pontile constituents is of particular interest as it indicates the transition from the pontile level of the stem to the diverging cerebral peduncles. A deep ventral sulcus in the pons indicates the position at which the divarication will occur, while at the junction between the basis and tegmentum in the midline, a small space marks the position of the foramen caecum anticum. The central gray matter (Cen) entirely surrounds the Sylvian aqueduct and in its ventromesial portion is specialized to form the trochlear nucleus, or nucleus of the fourth cranial nerve (N 4), whose emergent fibers are seen collected in a dense bundle occupying a posi-

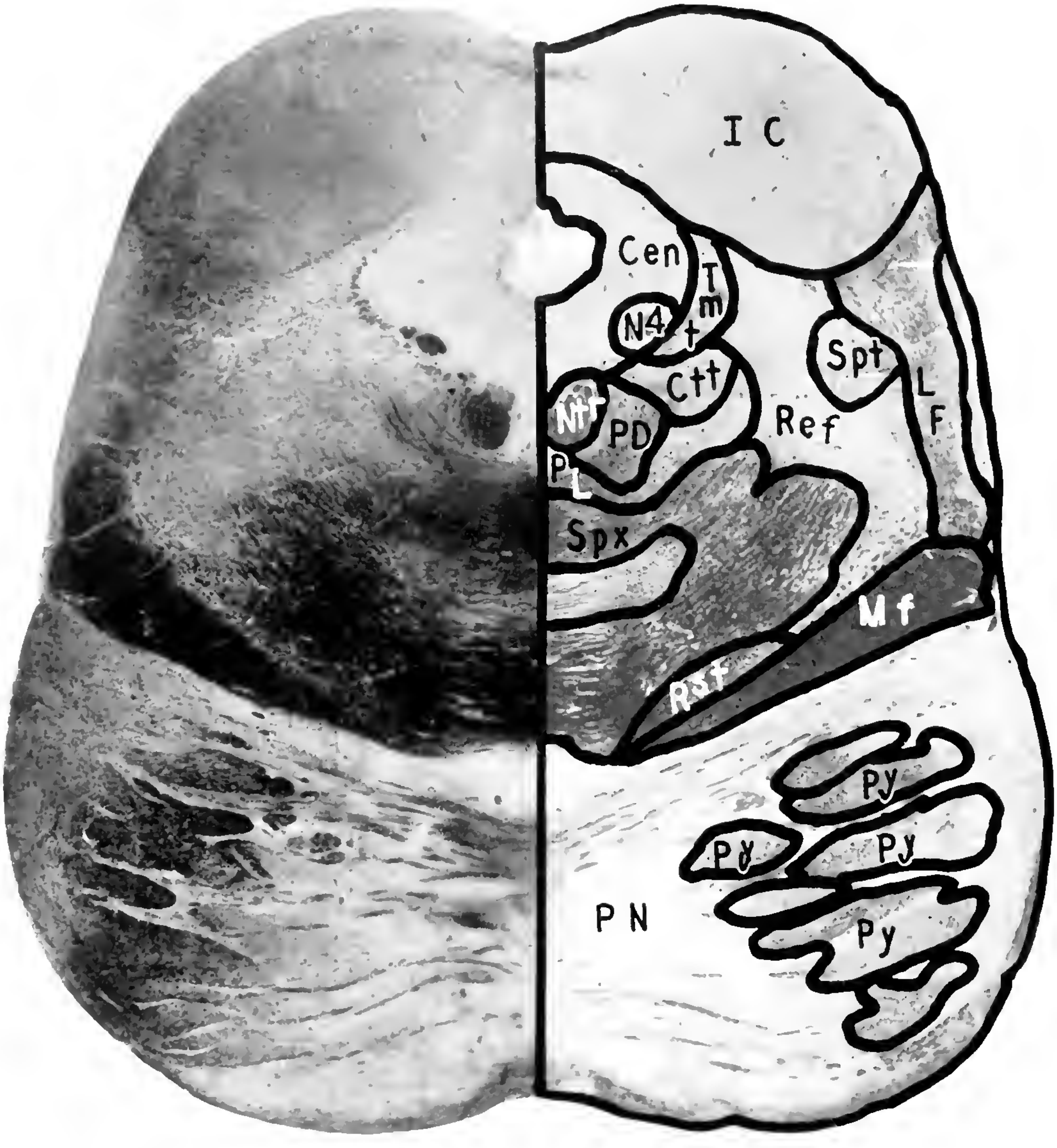


FIG. 238. ORANG-OUTANG. LEVEL OF THE INFERIOR COLLICULUS.

CEN, Central Gray Matter; CTT, Central Tegmental Tract; IC, Inferior Colliculus; LF, Lateral Fillet; MF, Mesial Fillet; NTR, Trapezoid Nucleus; N4, Trochlear Nerve; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PN, Pontile Nuclei; PY, Pyramid; RET, Reticular Formation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; SPX, Crossing of the Superior Cerebellar Peduncle; TMT, Tractus Mesencephalici Trigemini. [Accession No. 109. Section 504. Actual Size 19 × 19 mm.]

tion in the margin of the central gray matter. Laterally, the central gray matter contains the mesencephalic root of the fifth nerve and in a more ventral position are the dense bundles constituting the posterior longitudinal fasciculus (PL). The boundary line between the basis and tegmentum at this level is indicated by transversely disposed bundles forming the mesial fillet (Mf), lateral to which are the fibers constituting the large fasciculus of the lateral fillet (Lf), an important intermediary system of fibers in the auditory pathway. The most important structure at this level is, however, represented by the colliculus, as its specialization forms a relay station for the auditory sense. The colliculus is less prominent than in the lower vertebrates and considerably less so than in the lower and intermediate primates. It still retains many vestiges of its former histological specialization. A number of strata may still be discerned in it, reminiscent of its stratification in the inframammalian vertebrate.

LEVEL OF THE SUPERIOR COLLICULUS (FIG. 239)

At this level the section shows those changes peculiar to the appearance of the cerebral peduncles in the basal region and the elevation caused by the more cephalic prominences in the quadrigeminal plate. The superior colliculi (SC) appear as definitely specialized structures which microscopically show a faint degree of stratification. Their elevation is less pronounced than is the case in certain others of the primate series. From their general character the inference seems justified that the function which they represent, namely, vision, could at best be but ineffectually carried on by them. Their vestigial condition as compared with the lower vertebrates is so pronounced, both as to size and histological detail, as to suggest a decrease in functional activity. The process of visual delegation to the occipital lobe of the cerebral hemisphere, which in these studies has become so familiar a subject of discussion, is evident in the orang. The continuation of this telencephalization is carried to a still further extent in the higher anthropoids and man. Even in the primate order, therefore, this sign of evolutional progress in the nervous system is clearly manifest.

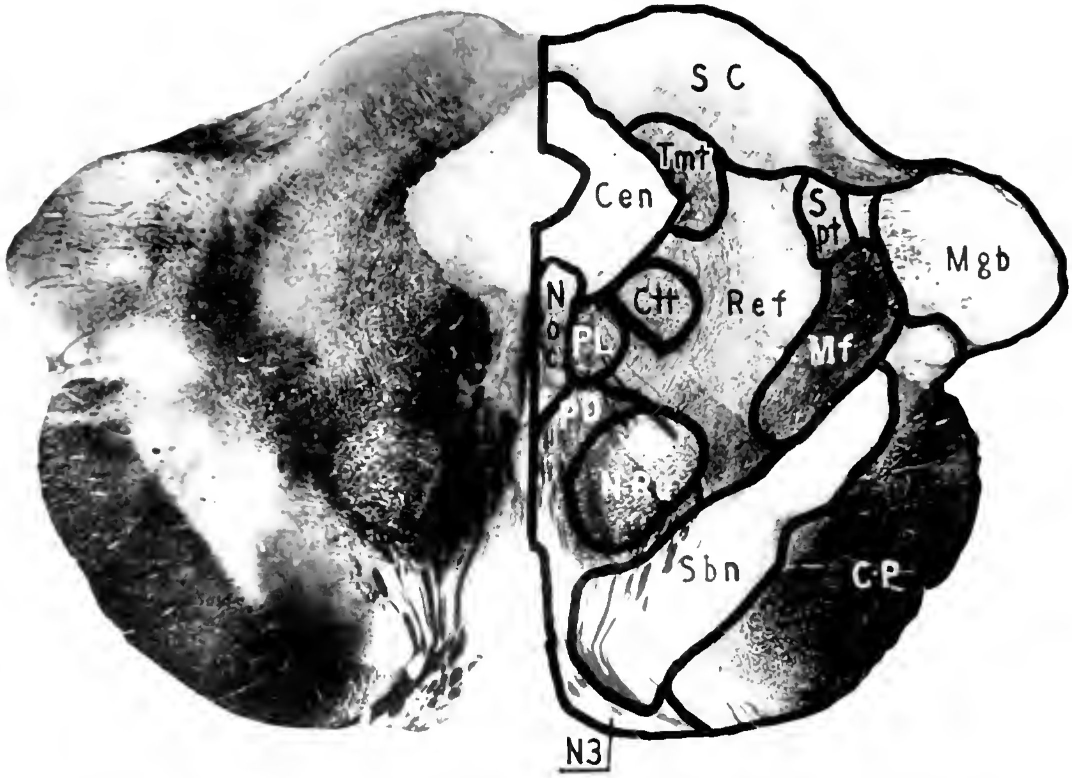


FIG. 239. ORANG-OUTANG. LEVEL OF THE SUPERIOR COLLICULUS.

CEN, Central Gray Matter; CP, Cerebral Peduncle; CTT, Central Tegmental Tract; MF, Mesial Fillet; MGB, Mesial Geniculate Body; NOC, Nucleus Oculomotorius; NRU, Nucleus Ruber; N3, Oculomotor Nerve; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; REF, Reticular Formation; SBN, Substantia Nigra; SC, Superior Colliculus; SPT, Spinothalamic Tract; TMT, Tractus Mesencephalici Trigemini. [Accession No. 190. Section 636. Actual Size 26 × 13 mm.]

The central gray matter (Cen) surrounds the Sylvian aqueduct, and in its more ventral portion becomes specialized to form the oculomotor nucleus (Noc). This nuclear collection is among the most important of the cranial nerve groups, not because the muscular territory over which it presides is extensive, but because the muscles themselves, however delicate and small, are capable of producing the most exactly adjusted of all movements in the body. Ocular movements are so minutely adapted to the function of vision, that the slightest deviation of the eyeball of one or both sides will disturb the process of visual fusion, or produce other defects in visual perception sufficient to disorganize the special sense of sight. The object of conjugating the eyeballs so that their visual axes shall remain in parallel, or be convergent to that degree necessary for the prompt binocular fusion in near vision, requires the most delicate of muscular mechanisms for its achievement. This activity, in addition to the immediate readjustments necessary to distant vision, exerts a far-reaching influence upon all neokinetic organization. There can be no question that vision operates as an essential, supplementary aid both in the acquisition and in the control of a vast number of highly skilled motor activities.

So important a musculature as that of the eyeballs requires a complicated nuclear structure for the final distribution of its innervating impulses. The visual distance receptors of the two eyes are in reality one organ in the primates; at least, they are dual only in the sense of their morphological organization. Physiologically their object is to give their possessor a unified impression of the world upon which he gazes, without reduplication, without distortion, without adventitious mobility. Since the two eyes, serving this purpose, act as a single organ, the two nuclei by which the eye muscles are motivated so operate in unison that they may be rightly considered a single nucleus. This unity in structural design of the oculomotor nucleus is determined by a close internuclear communication across the midline provided by a great number of crossing fibers which pass from one side to the other, the oculomotor, commissural and decussating axons. These fibers conjugate the oculomotor, nuclear groups on the right and left side and so produce the desired unity.

The internuclear communication between the two symmetrical divisions of the nuclei supplying impulses to the eye muscles depends upon the extent to which the commissural and decussating fibers are developed. Their extensive development in the orang denotes a unification of the visual process calculated to produce a high degree of binocular vision. The fibers of the oculomotor nerve (N 3) pass forward to the oculomotor sulcus, whence they emerge at the base of the brain in the opticeo-peduncular space. In their course they pass, some through and some around, a large nuclear structure which has differentiated in the ventromesial portion of the reticular formation and constitutes the red nucleus (N Ru). Not only the size but the clear definition of this nucleus in the midbrain shows a distinct advance in its organization as compared with the lower and intermediate primates. It supplies collateral evidence which, in conjunction with the increased size of the lateral lobes of the cerebellum, with the increased complexity of the dentate nucleus and with the increased size of the superior cerebellar peduncle, indicates that coordination has undergone considerable expansion in passing upward to this higher form of anthropoid. Such must necessarily be the case in view of the animal's high differentiation of upper extremity and hand. Compared with the gibbon, for example, the orang-outang employs the hand for many purposes much more humanoid in character and requiring the organization of a wider range of movement. The greater definition and larger size of the red nucleus in this form signifies an extension of coordinative control. The reticular formation is less extensive than in the lower forms and in its ventral portion contains the fibers of the mesial fillet (Mf). The latter separates the reticular formation (Ref) from a large nuclear mass extending obliquely across the dorsal aspect of the peduncle, the substantia nigra (Sbn). What the exact physiological significance of this structure may be is still in doubt, although the control of certain automatic associated movements has been attributed to it.

The basis of the cerebral peduncle (CP) is entirely medullary. It contains the bundles of fibers which make up the pyramidal tract and the pallio-ponto-cerebellar fiber systems. Nowhere in the brain is the relative importance of fiber systems more clearly indicated than in this instance. These two systems, both arising in the cerebral cortex, both expanding in volume, size and capacity as the cerebral cortex increases in the evolutional sense, both concerned with the efferent conduction of nerve impulses known to be closely associated with the regulation of motor performances, exceed in size all other similar systems of the neuraxis. Increments in the size of the basal portion of the cerebral peduncle are in direct proportion to expansions of areas in the cerebral cortex. Projection fibers arising in the neopallium, as, for example, those constituting the pyramidal system as well as those entering into the formation of the pallio-ponto-cerebellar system, denote the neokinetic capacity of the animal. The evidence afforded by the increased volume of the cerebral peduncle is susceptible of but a single interpretation, namely, that expansion has taken place in direct proportion to extensions in behavioral performance, due to the acquisition of more complex, more numerous and more varied motor activities. This phyletic history of the cerebral peduncle furnishes testimony in favor of a progressive evolution throughout the primate order.

At the lateral extremity of the reticular formation is a pronounced elevation, the mesial geniculate body (Mgb), which receives some fibers from the lateral fillet.

From the functional point of view this level signifies certain advances in the visual sense, which appear in the tendency to acquire more capacious areas for the extension of vision within its own sphere as well as its association with sensory impressions in other spheres, such as hearing and body sense. This midbrain level also denotes the progress in the exact conjugation of ocular movements for the purpose of binocular and stereoscopic vision.

LEVEL OF THE OPTIC CHIASM (FIG. 240)

At the level of the optic chiasm the brain has passed into its diencephalic portion which contains the third ventricle (V3), bounded upon either

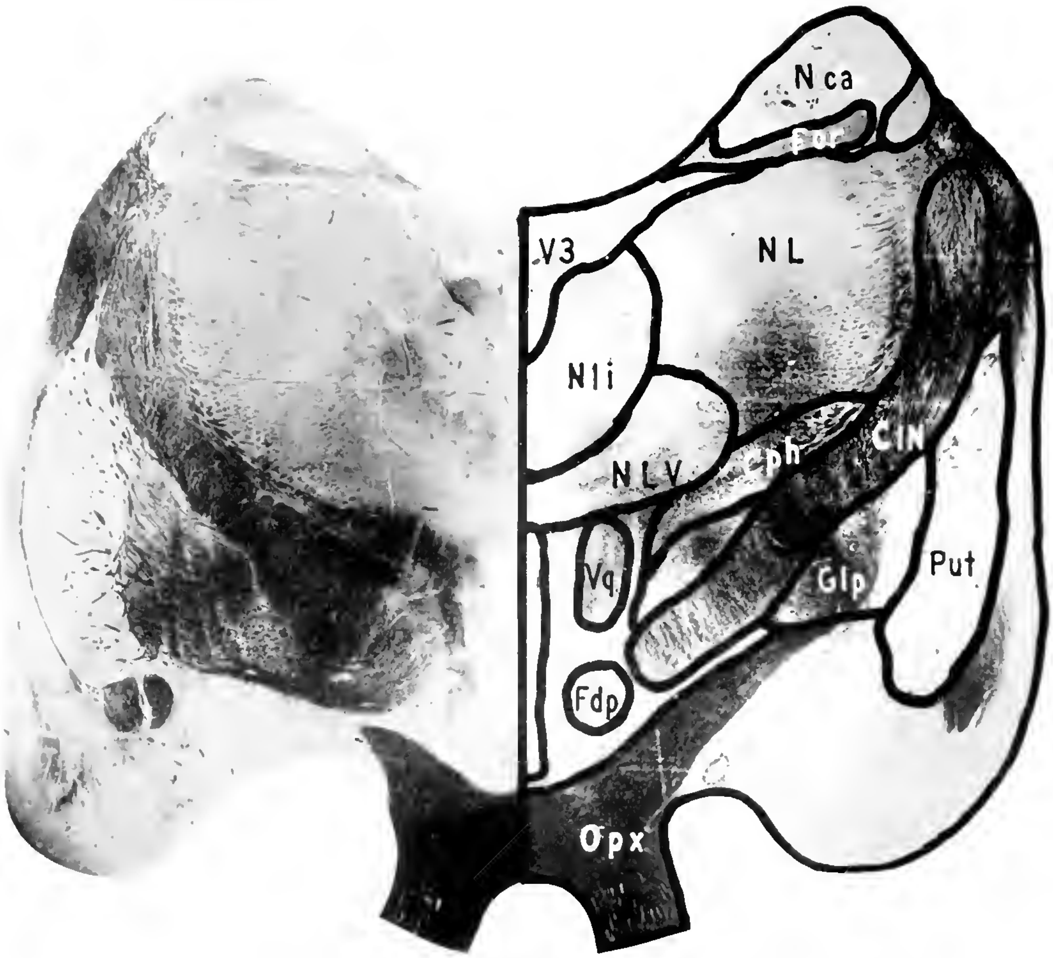


FIG. 240. ORANG-OUTANG. LEVEL OF THE OPTIC CHIASM.

CIN, Internal Capsule; CPH, Corpus Hypothalamicum; FDP, Descending Pillar of the Fornix; FOR, Fornix; GLP, Globus Pallidus; NCA, Caudate Nucleus; NL, Lateral Nucleus of the Thalamus; NLI, Internal Lateral Nucleus of the Thalamus; NLV, Ventrolateral Nucleus of the Thalamus; OPX, Optic Chiasm; PUT, Putamen; VQ, Fasciculus of Vicq d'Azyr; V3, Third Ventricle. [Accession No. 100. Section 754. Actual Size 42 × 20 mm.]

side by the optic thalami and bridged across by the commissura mollis. The optic chiasm (Opx) appears in the most ventral position of the section as a dense bundle of crossing fibers connected dorsally with the optic tracts and ventrally with the optic nerves. The optic thalamus is separated from the most ventral portion of the endbrain constituting the globus pallidus (Glp) by a dense bundle of fibers many of which occupied positions in the cerebral peduncle. This bundle of fibers is the internal capsule (Cin). Dorsal to the optic chiasm is a slight bundle of decussating fibers known as the supraoptic decussation of Meynert. The other structures of topographical interest in the section are indicated by appropriate letters in the caption accompanying the figure.

CHAPTER XVIII

RECONSTRUCTION OF THE GRAY MATTER IN THE BRAIN STEM OF SIMIA SATYRUS, THE ORANG-OUTANG

THE gray matter in the brain stem of the orang-outang in many respects resembles that in the human. The component structures have materially increased in size, their complexity is greater and the entire organization of the central nervous system shows a distinct advance over the lower primate forms.

In the high cervical levels of the spinal cord the configuration of the gray matter is identical with that in the human cord. The central gray matter is more or less quadrilateral in shape, connected at its ventrolateral angle with the ventral gray column. Extending from its dorsolateral angle is the narrow cervix of the dorsal horn which is capped by the substantia gelatinosa Rolandi. The dorsal sensory nuclei have already made their appearance in the dorsal columns, although the distal portion of the nucleus of Goll is not yet connected with the central gray matter. It is represented by a narrow, compressed strip of gray matter lying in the ventrodorsal plane close to the midline, completely surrounded by fibers of the column of Goll. The dorsal horns are already showing their tendency to move into a lateral position. This tendency is shown more by the lateral inclination of the extremity of the dorsal horn than by the cervix. On the lateral side of the ventral gray column the reticular formation appears as a small triangular area.

THE DORSAL SENSORY NUCLEI

The nucleus of Goll appears in the first levels of the reconstruction as an independent, compressed band of gray matter lying among the fibers of the column of Goll. It quickly establishes connection with the dorsal surface of the ventral gray matter and continues upward as a flat strand showing but little inclination to increase in size. Upon the first appearance of the nucleus of Burdach, the nucleus of Goll shows definite and marked expansion in its dorsal extremity. It increases in size laterally so that its outline presents a tree-like appearance, the branches of which are directed laterally from the dorsal midline. The nucleus soon occupies almost the entire area of the column of Goll.

The nucleus of Burdach appears as a small, sessile condensation in the dorsal surface of the central gray matter, lateral to the base of the nucleus of Goll. It expands rapidly in size and is displaced laterally by the increasing bulk of the nucleus of Goll. The entire dorsal nuclear mass begins to show the effects of the opening of the fourth ventricle. A marked displacement takes place in the dorsal sensory nuclei, as is evidenced by the lateral shifting of these nuclear masses. The nucleus of Burdach becomes arborescent in appearance, its dorsal surface overhanging the substantia gelatinosa trigemini which lies ventral and somewhat mesial to it. The nucleus of Goll continues upward beyond the opening of the fourth ventricle, forming a part of its lateral mass. At about the caudal level of the fourth ventricle it begins to decrease and it rapidly is submerged from view by the approximation of the lateral mass of the fourth ventricle and the dorsal aspect of the nucleus of Burdach. This latter nucleus continues upward to a little above the mid-point of the ventricle, where it begins to decrease in size and then disappears to give place to the vestibular complex. This complex extends upward in approximately the same topographical relation as that shown successively by the nucleus of Goll and the nucleus of Burdach.

The substantia gelatinosa trigemini occupies a position which indicates its continuity with the substantia gelatinosa Rolandi of the spinal cord. Passing upward into the oblongata, it assumes its lateral position. In the lower levels the direction of the gelatinous cap is more or less transverse, but as the structure is followed upward into the stem the nuclear mass undergoes a partial rotation until its dorsal surface is directed towards the lateral periphery of the oblongata. The constriction which was found to be almost con-

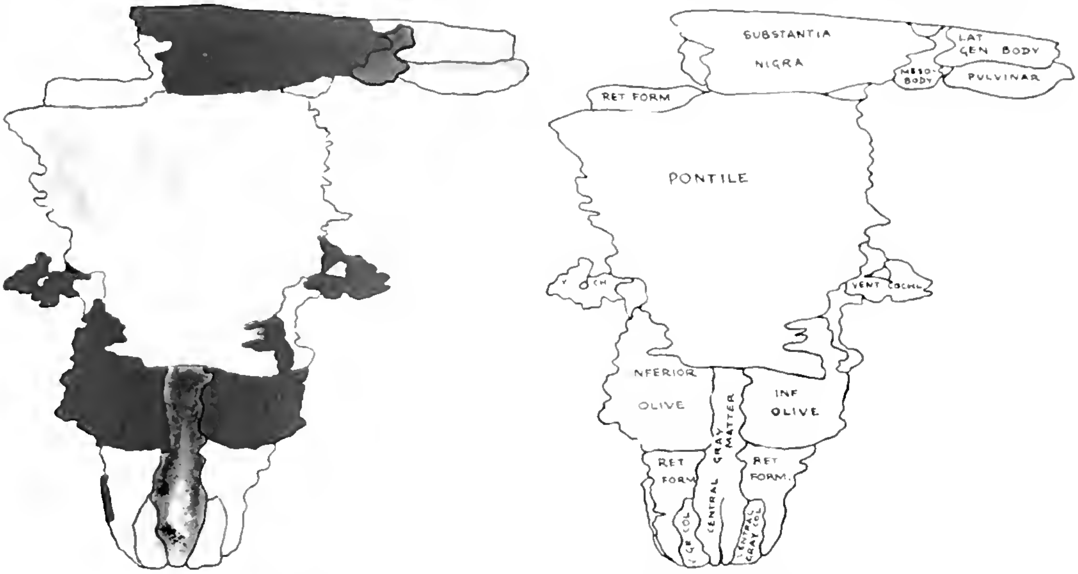


FIG. 241. VENTRAL SURFACE OF GRAY MATTER OF BRAIN STEM, SIMIA SATYRUS. KEY TO DIAGRAM. INF. OLIVE, Inferior Olive; LAT. GEN. BODY, Lateral Geniculate Body; MESO-G. BODY, Mesial Geniculate Body; PONTILE, Pontile Nuclei; RET. FORM., Reticular Formation; V. CH. and VENT. COCHL., Ventral Cochlear Nucleus; V. GR. COL. and VENTRAL GRAY COL., Ventral Gray Column.

stant in the conformation of this nuclear mass is not so well defined in Simia satyrus as in the other species. It is faintly indicated at the mid-ventricular level of the stem. The substantia gelatinosa trigemini continues upon the surface of the reconstruction to a point which corresponds approximately to the closure of the pontile ventricular cavity. Here it expands to form the caput of the nucleus and at this point comes into relation with the motor nucleus of the trigeminal nerve.

THE INFERIOR OLIVARY NUCLEUS

The inferior olivary nucleus in the orang-outang assumes considerable complexity and bulk. The fundus of the nucleus is broad and disposed toward the ventrolateral angle of the neuraxis. It begins just below the level of the fourth ventricle, extending its two branches mesially and somewhat dorsally toward the median raphe. Both the dorsal and the ventral branches show marked reduplication. The ventral accessory olivary nucleus begins at the level in which the main nucleus arises. It extends upward as a flat band applied to the ventral aspect of the main nuclear mass. It approaches the cephalic limit of the main nucleus, becoming continuous with the dorsal extremity of the ventral branch near its summit. The dorsal accessory olivary nucleus begins below as an inconspicuous mass at about the same level as the main olivary nucleus. It rapidly extends in a ventrodorsal direction, lying as a flat band dorsal to the mesial half of the dorsal branch of the main nucleus. At the cephalic extremity of the principal nucleus it becomes confluent with the dorsal extremity of the dorsal branch. The entire complex extends as far upward as the midventricular level of the brain stem, where it disappears by merging with the reticular matrix. Its ventral surface is in contact with the pyramidal tract and the ventral portion of the mesial fillet. Its fundus is covered only by the external arcuate fibers, while its dorsal surface is in contact with the ventral surface of the reticular formation.

The Reticular Formation

At a point slightly above the lowest sections of the reconstruction, the ventral gray column becomes detached from the central gray by the decussating pyramidal fibers. This gray column is soon replaced by the reticular formation with which it merges and eventually disappears. The reticular formation itself is seen in the lowest levels of the reconstruction as a small collection of mixed gray and white matter on the outer surface of the ventral gray column. This rapidly increases in size as it is followed upward. It extends dorsad to come into contact with the substantia gelatinosa Rolandi.

Ventrally and laterally it passes toward the ventrolateral angle of the tegmentum. The dorsal surface of the reticular formation becomes broad and is intimately connected with the ventral surface of the central gray

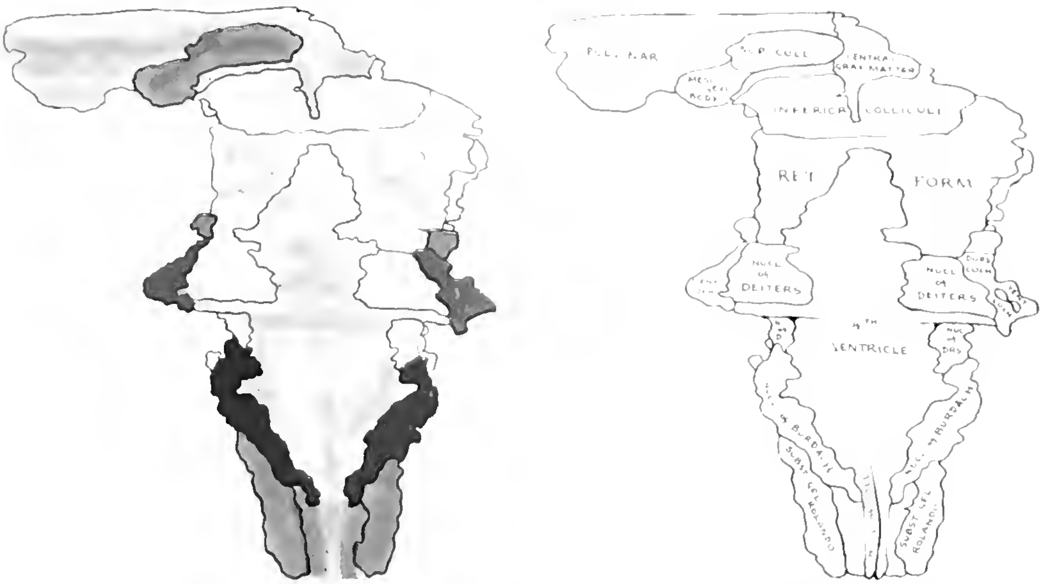


FIG. 242. DORSAL SURFACE OF GRAY MATTER OF BRAIN STEM, SIMIA SATYRUS.

KEY TO DIAGRAM. DORS. COCH., Dorsal Cochlear Nucleus; MESO-GEN. BODY, Mesial Geniculate Body; NUCL OF BURDACH, Nucleus of Burdach; N. OF D., NUC. OF DRS. and NUCL. OF DEITERS, Nucleus of Deiters; NUCL. OF GOLL, Nucleus of Goll; RET. FORM., Reticular Formation; SUBST. GEL. ROLANDO, Substantia Gelatinosa of Rolando; SUP. COLL., Superior Colliculus; VENT. COCH., Ventral Cochlear Nucleus.

matter which is now flattening out. The reticular formation gradually increases in bulk, forming the chief nuclear mass of the tegmentum in the upper oblongatal and pontile regions. It embraces in these levels the dorsal surface of the inferior olivary complex. Dorsal to the reticular formation lie the nucleus of Burdach and the nucleus of Goll, together with the increasing mass of the vestibular complex. The reticular formation comes into contact with the ventral surface of the central gray matter forming the floor of the fourth ventricle.

The mesial surface of the reticular formation throughout its entire extent is more or less smooth and separated from its fellow of the opposite side by the longitudinal fiber tracts near the raphe. Above the level of the substantia gelatinosa trigemini, and the vestibular and cochlear complexes, the reticular formation expands and forms almost the entire mass of the tegmentum of the upper pons and mesencephalon. It reaches the surface and sends a number of prolongations backward, one of which forms an investment over the superior cerebellar peduncle as this fiber tract approaches the mesencephalic tegmentum. Ventrally the reticular formation comes into close contact with the dorsal portion of the lateral buttress of the pontile nucleus. Laterally and mesially it is in contact with the mesial buttress, while between teshe two points of apposition the ventral surface of the reticular formation and the dorsal surface of the pontile nucleus are separated by the trapezoid body. In the mesencephalon the reticular formation is irregular in outline. It is penetrated from behind forward by the superior cerebellar peduncle which gradually sinks deeper into the tegmentum, thus allowing more of the reticular formation to form on its lateral aspect. The development in the mesencephalon of the nucleus ruber presents a massive condensation in the reticular formation. The reticular formation of the mesencephalon, followed upward toward the point of transition into the diencephalon, demonstrates the continuity of these two structures, the reticular formation of the mesencephalon merging with the indifferent zona incerta of the interbrain. The lateral surface of the reticular formation in the lower mesencephalic area is crossed from before backward by a depression produced by the passage of the lateral fillet. In the intercollicular region a continuation of the formatio reticularis passes dorsally and mesially to separate the two colliculi. In the most cephalic portion of the midbrain the reticular formation gives origin to a similar dorsal prolongation which separates the superior colliculus from contact with the nuclear masses of the epithalamus and metathalamus.

The Pontile Nuclei

This nuclear mass is very much more complicated than in any of the lower primates. Although much more intricate, the arrangement is identical

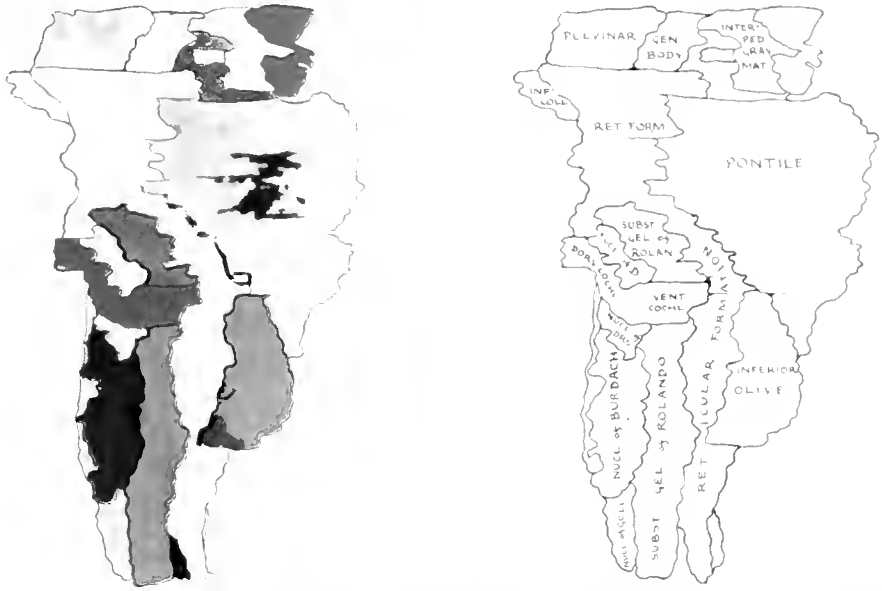


FIG. 243. LATERAL SURFACE OF GRAY MATTER OF BRAIN STEM, SIMIA SATYRUS. KEY TO DIAGRAM. DORS. COCHL., Dorsal Cochlear Nucleus; GEN. BODY, Geniculate Body; INF. COLL., Inferior Colliculus; INTERPED. GRAY MAT., Interpeduncular Gray Matter; NUCL. OF BURDACH, Nucleus of Burdach; NUCL. OF D. and NUCL. OF DRS., Nucleus of Deiters; NUCL. OF GOLL, Nucleus of Goll; PONTILE, Pontile Nuclei; RET. FORM., Reticular Formation; SUBST. GEL. OF ROLAN. and SUBST. GEL. OF ROLANDO, Substantia Gelatinosa of Rolando; VENT. COCHL., Ventral Cochlear Nucleus.

with that found in lower forms. The presence of the superficial layer corresponds to the general configuration and curves of the brain stem. The deep layer is in contiguity with the superficial surface of the reticular formation as well as with the two buttresses which serve to connect the superficial and the deep layers of the nuclear substance at their extremities. The arciform nuclei are relatively well defined, beginning at about the mid-olivary region as strips of gray matter disposed along the mesial and ventral surfaces of the pyramid. These strips continue upward, gradually increasing until a complete sheath is formed around the pyramid. The pontile nuclei fuse at the midline. Passing through the cavity of the nuclear sheath are strands which produce the numerous bridges of gray matter separating the pallio-spinal and pallio-pontile fibers into smaller groups. The dorsal portion of the lateral buttress is in contact with the ventrolateral angle of the reticular formation and a similar arrangement presents itself in regard to the dorsal part of the mesial buttress. The dorsal surface of the deep layer of the pontile nuclei and the ventral surface of the reticular formation are not in actual contact on account of the development at this point of the various longitudinal fibers. The pontile nuclei begin to diminish as the isthmus is approached and rather rapidly come to a termination. The superficial layer, together with the lateral and mesial buttresses, first begin to diminish and then disappear, leaving the deep nuclear layer to continue upward and become confluent with the substantia nigra. The latter seems, therefore, to be supported by the upper extension of the two buttresses and throughout its extent by the deep layer of the pontile nuclei.

The Vestibular Complex

The vestibular complex first appears as a small triangular collection of nuclear material located between the lateral aspect of the floor of the fourth ventricle and the upper dorsal portion of the nucleus of Burdach. It rapidly expands in size, acting as a wedge which serves to separate the ventricular floor from the latter nucleus. A prolongation is carried forward ventrally, which separates the inferior cerebellar peduncle from the pontile tegmentum.

At the mid-ventricular level and dorsal to the nucleus of Deiters, the nucleus triangularis of Schwalbe appears. It lies beneath the floor of the ventricle. This nuclear mass continues upward to a point at which the ventricle begins to close, where it rapidly terminates. The triangular nucleus in the mid-ventricular level is separated from the ventricular gray matter by the dorsal cochlear nucleus, together with the striae acusticae which cross it to enter the lateral recess of the fourth ventricle. The nucleus of Bechterew is continued dorsally from the vestibular complex into the lateral wall of the fourth ventricle and is well shown in the reconstruction.

The Cochlear Complex

The cochlear complex is relatively insignificant. The ventral cochlear nucleus is so disposed as to present a trough which receives the entering fibers of the cochlear nerve, which thus is surrounded on its ventral, lateral and dorsal aspects. The mesial aspect of the nerve is in contact with the restiform body and the tegmentum of the metencephalon.

The dorsal cochlear nucleus is also relatively inconspicuous. It is connected with the ventral cochlear nucleus by strands of gray matter and also by the fibers which make up the entering cochlear root.

The Colliculi

The inferior colliculus appears as a condensation in the dorsal mesencephalic reticular formation and is of somewhat greater size than is found in the lower forms. This increase in size, however, is dependent only upon the general increase in bulk. The colliculus seems to be of relatively less extent and significance in this form than it is in those already described. It is supported laterally by the lateral extension of the mesencephalic reticular formation, whereas dorsally it rests on the undifferentiated median gray matter. It is separated from the superior colliculus by a lateral extension from the reticular formation which passes dorsomesially in the intercollicular sulcus.

The superior colliculus is of moderate size, resting laterally upon the reticular formation and dorsally upon the dorsai median undifferentiated gray matter. Its median extremity is disposed similarly to that of the inferior colliculus and is transversed by the formation in this region of the intercollicular commissures which join the inferior colliculi and the superior colliculi respectively. The superior colliculus is separated from the diencephalic structures by another dorsal extension of the mesencephalic reticular formation.

The Substantia Nigra

The substantia nigra appears at the transition between the metencephalon and the mesencephalon. It seems to be a specialization from the deep layer of the pontile nuclei and is supported by the lateral and mesial buttresses. Its ventral surface is in direct relationship with the descending pallio-spinal and pallio-pontile systems of fibers. Mesially it is continuous with the indifferent interpeduncular gray matter from which it is separated by the emerging fibers of the oculomotor nerve. It expands laterally as far as the reticular bed containing the mesial and lateral geniculates. Dorsally it lies in relationship with the ventral surface of the mesencephalic reticular formation. As the diencephalon is approached it diminishes in extent and finally disappears, seeming to give place to the zona incerta.

The Nucleus Ruber

The nucleus ruber appears at about the level of the oculomotor nucleus as a rounded, well-demarcated specialization in the mesial portion of the mesencephalic reticular formation. It rapidly increases in size to its maximum and then as rapidly diminishes. It is surrounded at all points and separated from the reticular formation by the encapsulating fibers derived from the superior cerebellar peduncle.

The Central Gray Matter

The central gray matter has already been described in connection with the upper cervical levels and there presents the quadrilateral form which is found in the human brain stem. It presents the usual four angles: the ventrolateral receiving the ventral gray columns, and the dorsolateral receiving the dorsal gray columns. As the oblongata is approached the central gray matter gives rise to the dorsal medullary nuclei, the nucleus of Goll appearing shortly after the upper levels of the cervical region are passed. The nucleus of Burdach appears at a considerably higher level. As these nuclei develop the central gray matter becomes more flattened from side to side and continuously approaches the dorsal surface of the stem. This is very clearly shown by the diminishing anteroposterior extent of the dorsal medullary nuclei. The central gray matter in the mid-oblongatal region sends out a narrow prolongation dorsally which, reaching the surface, bifurcates and extends laterally. The remainder of the central gray apparently follows the lead of this extension, passing dorsally and flattening out laterally until the floor of the fourth ventricle is formed. The floor of the fourth ventricle in the orang begins to show somewhat more modelling than in the preceding types. The suggestion of the hypoglossal and the vagal trigones may be discerned in the lower half of the fourth ventricle. The area acustica is fairly well developed, crossed by the striae acusticae. In the upper portion of the ventricle the medianly placed elevations corresponding to the development beneath them of the nucleus abducentis with the knee of the seventh nerve are well marked.

Above the mid-ventricular level of the stem the ventricle rather rapidly narrows by the approximation of its walls. As the junction with the mesencephalon is passed, the walls of the aqueduct of Sylvius, formed by the central gray matter, become progressively more massive. In the mesencephalon itself the central gray is continued forward as a fairly well-defined tongue lying on either side of the median raphe. In this region develop the nucleus trochlearis and the nucleus oculomotorius. Above the level of the oculomotor nucleus the ventral prolongation of the central gray matter is continued forward, indicating the approach of this structure toward the third ventricle. When the third ventricle is reached this prolongation becomes continuous with the subependymal gray matter and the mesial group of the diencephalic nuclei.

Chapter XIX

TROGLODYTES NIGER, THE CHIMPANZEE, ITS BRAIN AND BEHAVIOR

Its Position among the Primates; Measurements and Brain Indices; Surface Appearance of the Brain; Internal Structure of the Brain Stem in Cross Section

THE chimpanzee, although usually referred to the genus of Pan, is sometimes described as Simia, which appears to be an older designation. It occupies a position among the great anthropoid apes intermediate between the gorilla and the orang-outang.

Appearance of the Chimpanzee

In point of size it is somewhat larger than the orang, but smaller than the gorilla. Depending upon its species, the animal varies in height from something over three feet to a little over four feet. In color it is a blackish-brown with rather thick hair over the entire body except the face and brow. In some species the scalp is bald. The chimpanzee possesses great strength and agility. In spite of its relatively short stature, it is more than a match even for the strongest man. Its body is short, usually with a protuberant abdomen. The legs are also short, and compared with the upper extremity, they appear even shorter. The foot is short with a great toe which is thick and opposable. The other toes are united by a web near their bases. The arms are long, reaching for a considerable distance below the knees when the animal stands erect. The hands are broad; the thumb is short and the fingers are united by a web at their bases, as in the case of the toes. The middle finger is the longest. Callosities develop on the dorsal surface of the fingers in consequence of "knuckle" walking and running which the animal does mostly upon all fours, using the back of the hands for support. The nose is somewhat depressed, with nostrils opening downward. The lips are mobile and protrusive, the ears are large and extend above the skull. The lower jaw protrudes; the canines are long and conical. In the upper extremities, the humerus nearly equals the length of the radius. The female is somewhat smaller than the male and bears one young at a time, which she carries in passing through the trees and over the ground in the manner characteristic of other apes.

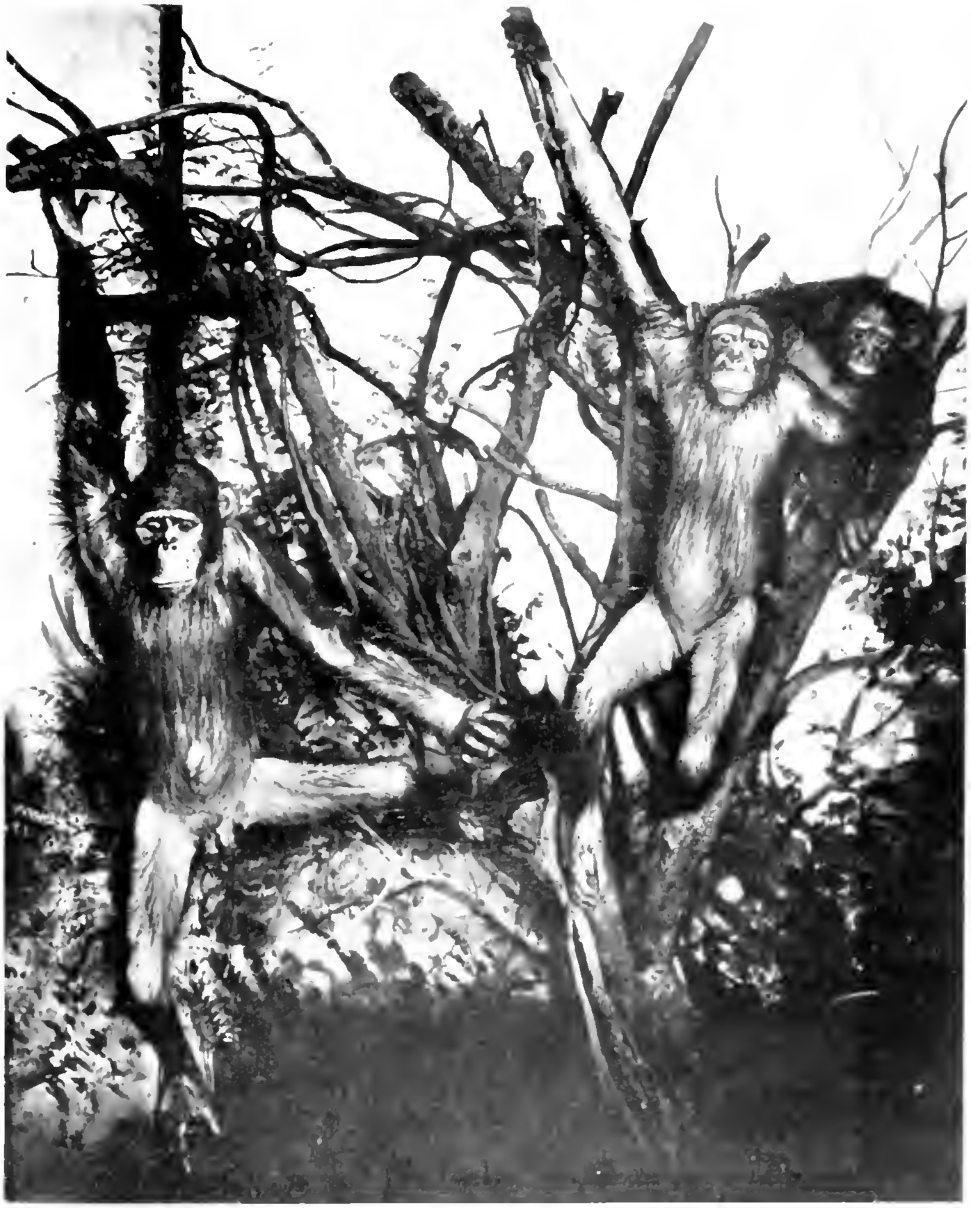
Habits of the Chimpanzee

Some nine or ten species have been more or less definitely identified as belonging to this genus. The species here described is Pan satyrus (Troglodytes niger). This animal inhabits lower Guinea, Cenaga to the Ogowe, Semikaro Desumland near the Cenaga in the Cameroon, Yayundi and Difundi in the Cameroon and Mayumba.

Concerning the habits of the animal in its native state, little is known of any of the species of chimpanzee. It is fortunate that many of these animals have been captured when very young and not a few have been made the subject of careful psychological and behavioral studies. Möbius was apparently the first to make systematic observation of the behavior of the chimpanzee, in 1867. Other animals of this genus have been the subject of psychological investigation by Witmer in 1910, Romanes, 1900, Hirschlaff, 1905, Shepherd, 1915, and Hobhouse in 1915.

KÖHLER'S BEHAVIORAL RESEARCH UPON THE CHIMPANZEE

Undoubtedly the most carefully controlled behavioral research yet made is that of Professor Köhler, working at Teneriffe in the Canary Islands, under the auspices of the Prussian Academy of Science which had established at this place a well-equipped anthropoid station. Nine chimpanzees were constantly under the observation in ideal conditions for study by



Courtesy, American Museum of Natural History

FIG. 244. HABITAT GROUP, CHIMPANZEE.

Köhler for a long period of time between 1914 and 1916. Köhler's purpose in this work was to test the intelligence of the higher apes and the methods applied by him are what he called the "roundabout methods" (Umweg),

Courtesy, New York Zoological Garden

FIG. 245. CHIMPANZEE SUSIE.

which so complicated ordinary situations as to require intelligent solutions on the part of the animal. Thus one of the most gifted animals of the collection (it may be noted that chimpanzees, as well as more highly organized personalities, differ in their individual ability to a very considerable degree) was given the following problem which was not altogether simple, and yet was more or less readily solved by the ape without unnecessary delay. From the roof of the animal's playground, a basket of bananas was suspended by means of a string passed through an iron ring. The end of the string was tied

Courtesy, New York Zoological Garden

FIG. 246. CHIMPANZEE SUSIE.

in a noose which, in turn, was placed over the limb of an old tree at the height of about three meters from the ground. The chimpanzee, Sultan, was then admitted into the playground. He was familiar with this basket and associated it with feeding time. On entering the enclosure, Sultan saw the basket at once and soon showed signs of considerable agitation because he was, contrary to custom, alone in the open. Manifesting his feelings in the usual chimpanzee style, he expressed his disapproval by making a thundering noise with his feet against the wooden wall of the apehouse, and at the same time tried to get in touch with the other animals by climbing up to the windows. At length he ceased these ineffective measures, and seeing the basket again, made for the tree, climbed quickly up to the noose, paused a moment while watching the basket, pulled the string until the basket bumped against the ring in the roof, released the string, pulled it a second time even more vigorously so that the basket turned over and a banana fell out. The chimpanzee then came down from the tree, but soon ascended once more now to pull quite violently until the string broke and the whole basket fell to the ground. He then clambered down, took the basket and went off to eat the fruit. Thus Sultan, in a relatively short time, had solved this roundabout problem by obtaining his objective in spite of the obstacles placed in his way.

Although many experimental tests were made to estimate the degree to which chimpanzees are capable of using implements, in the main such experiments are not necessary in order to induce the animal to handle objects in his immediate surroundings in a variety of ways. He has large and powerful as well as flexible hands which serve as the most natural and useful link between him and the world of things outside. Besides this, he obtains the necessary amount of muscular strength and coordination at an early age of development, much earlier than a human child. His feet, although far from being a second pair of hands, may still be used in emergencies in which the feet of the human races would be quite useless. Furthermore, the jaws and teeth are also serviceable, as is the case among many African tribes and other primitive people, though it may be to a less extent than with the anthropoid apes. The casual, every-day handling of objects by the chimpanzee comes almost entirely in the nature of play. In certain instances under the pressure of need, or compelled by the special circumstances of experimental tests requiring the use of objects or implements, it appears that the new knowledge acquired for using objects at play will be utilized to obtain some more definite objective. Primarily this object may have been employed without the slightest idea of an immediate gain and only to increase the joy of living. Later, however, it becomes of great practical utility for purposes serving the needs of the animal. Thus, jumping by means of a stick or pole, which was invented de novo by one of the chimpanzees in the group and soon imitated by others as a means of entertainment, was soon put to a more practical use in obtaining food which had been suspended above them and out of reach unless they resorted to some means of elevating their bodies into closer proximity to the desired goal. So that in the end this improvised mode of modified pole vaulting became a regular procedure among the chimpanzees in the business of obtaining food put out of their reach over their heads.

The animals also used straws and twigs in the manner of spoons, at first more or less in play during meal time especially after their first thirst had been quenched, and they liked to amuse themselves by dipping the water up with a straw and sucking the straw. On one occasion some red wine was poured into the drinking water which they shared in common. On the first taste of the new mixture they all paused for a minute, then one of the chimpanzees began to spoon up this novel drink with a straw, and all of the others immediately followed his example with twigs and similar straws. In thus acquiring the use of twigs and straws as spoons there could have been no possible imitation, for none of them had had as yet a chance of seeing a human being use a knife, fork or spoon while eating. The twig or stalk was also employed quite deftly in other ways, combining with its usefulness as a table utensil some of the properties of a weapon of the chase.

In the summer time, a species of ant infests the portion of the Canary Islands where these great apes were housed. These ants passed in a wide stream, moving along over the beams around the wire netting which encircled the playground. The chimpanzee, having a special liking for acid fruit, which he prefers to all others, no doubt for this reason relished the formic acid of the insect. Usually upon seeing the ants, the chimpanzee simply rolled his tongue along the beam over which they were crawling and thus gathered them in for himself. If the wire netting intervened between him and the coveted delicacy, such a primitive method of capture would not suffice. So all of the chimpanzees soon learned to use sticks and straws which were thrust through the meshes of the wire netting and held in such

Courtesy, American Museum of Natural History

FIGS. 247 AND 248. HAND AND FOOT OF CHIMPANZEE.

LEFT. Palmar surface of hand, showing arboreal specialization. The thumb is short, the fingers are long, thenar and hypothenar eminences are pronounced.

RIGHT. Plantar surface of the foot showing definite humanoid tendencies, broad heel, distal advance of great toe, shortening of lesser toes, broadening of sole. The foot in chimpanzee has less of the hand-like characters observed in the lower primates.

position until they were covered by ants. The straws were then withdrawn and the insects promptly licked off and devoured. This method of capture proved most satisfactory and entertaining to the anthropoids. Their attention was entirely absorbed in this novel method of overcoming an obstacle unintentionally placed between them and the delicate morsels which they craved, but which would have been out of their reach had it not been for their recourse to this procedure.

If a mouse or lizard or small crawling animal entered the playground with the chimpanzees, it at once became the object of much excited interest, yet the big animals always hesitated to make a capture by a sudden snatch

Courtesy, American Museum of Natural History

FIGS. 249 AND 250. HAND AND FOOT OF CHIMPANZEE.

LEFT. Dorsum of the hand showing definite arboreal specializations.
RIGHT. Dorsum of foot showing prehensile specialization in the region of the great toe and shortening of the lesser toes.

with the naked hand. It was almost amusing to see the apes stretch their hands out with the intention of seizing the prey, with the fingers pointed, and then all at once draw back again quickly. A firm, quick grasp on these little wriggling animals appeared almost as impossible to them as to many people. Nearly every movement on the part of the poor quarry was followed by a nervous gesture. The caution and hesitation of the apes manifested, throughout the entire performance, the repugnance of touching the little creature with the unaided hand. Finally the chimpanzees learned to use sticks upon these small intruders of their domain and with such weapons, if the victim did not escape, at length despatched it, not, it would appear, in any spirit of cruelty, but more in the sheer excitement of pursuit and capture.

Professor Köhler also had opportunity to observe the rapidity with which the chimpanzees resort to the use of sticks when they encounter a new object for the first time in their lives. This was especially apparent upon their introduction to the electrical current. In the experiment, one pole of an induction coil was fastened to a wire basket filled with fruit and this suspended from the roof, while the other pole was connected with the wire netting upon the ground. In a very short time the chimpanzees manifested a great number and variety of entirely human reactions and expressive movements in response to this new condition. When contact was made by one of the great apes with the basket and the wire netting at the same time, there followed an immediate bounding back as the first shock was received. The cry of surprise or dismay, the cautious second attempt, the constant jerking backward before there was any possibility of the current passing through the body, the violent shaking of the hand in the air after receiving a shock, all of these were so exactly similar to the behavior of a human being who has inadvertently touched a hot stove, as to leave no doubt as to the resemblances in behavioral reactions under corresponding circumstances. Most of the reactions of the chimpanzees might easily find counterparts in the human being, quite as marked in one as in the other. It seemed almost astonishing to observe in these apes the number and variety of automatic responses to unexpected and even painful stimuli, which may be universally observed in man as well. Such responses must have taken their origin a long way back in the dark ages when the anthropoid and the human kind were beginning to emerge from some common ancestral stock.

In the further manipulation of objects the chimpanzees showed a tendency to develop additional habits. They did not eventually confine themselves to thrusting and hitting with sticks alone, but began to throw them. In moments of great joy, when very good food was being provided, one of the animals often seized another and shook him out of sheer pleasure. At first one of the animals would take a stick under such provocation and fling it vehemently at one of the chimpanzees in his or her proximity. This also frequently happened in play, particularly with the athletic female Chica, who was in the habit of creeping up behind one of her companions as they sat quietly at rest and, from fairly close quarters, hurling a stick, and then taking flight. From throwing sticks it was but a short step to using handfuls of sand in this manner, and finally stones of varied size and weight. At first the chimpanzees were not expert in these ballistic activities. Being deficient in the coordination of hand, head and eyes, they did not succeed in very accurate aim. Soon the throwing of stones became such a ruling passion among the chimpanzees that some of them became dangerously expert, particularly the gymnastic Chica, who learned to aim excellently and expressed her skill with equal satisfaction upon her fellow apes as well as her human associates.

These performances, which were largely in the nature of play and amusement, were by no means the only ones by which the chimpanzees showed a strong tendency for manipulating with considerable skill objects in their surroundings. All of the animals made nests, and this was true from the early periods of infancy onward. The full-grown chimpanzee, as might be expected, particularly the full-grown female, has the best results in this nest-building and really does most remarkable work in this line. Usually in the evening, a heap of straw is carefully manipulated while the animal sits inside and begins to twist the ends of the straw together. This work will continue all around the edge until an actual nest is formed which is not unlike that of the stork. A blanket may often be interwoven with the straw, or used as a cover over it. The younger animals, in their nest-making, are less tidy and exact. They seldom make so neat a turning down of the outer edges. But, on some occasions when they apparently take more pains with their handiwork, their movements during the preparation of the nest are exactly like those of the older females and the results closely approximate those of the more efficient workers. The nests are often made during the day in pure fun, and many different materials, such as string, grass, branches, rags, ropes and even wire collected for this purpose, not, however, when a nest is needed to sleep in, but only as a pastime when other objects of interest are lacking.

Objects of many kinds interested the chimpanzees, and they were not only intent upon the manipulation of them but seemed particularly fond of carrying quite a widely different variety of rubbish about on the body in one way or another. Nearly every day animals could be seen walking about with a rope, a bit of rag, a blade of grass or twig upon their shoulders. Some of them, if given a bit of metal chain, would put it about their necks quite in the manner of a necklace. Bushes and brambles were often carried in considerable quantities, spread out over the entire back, and twigs and pieces of grass were commonly seen hanging over their shoulders to the ground or on both sides of the neck. One of the animals contracted the habit of carrying about empty preserve cans, by taking the side that was open between his teeth, while one of the more sturdy of the group took a fancy at one time for carrying heavy stones about on her back. She began with a stone of four pounds but soon reached a much larger block of lava weighing nine pounds. Most of this occupation is carried on as play from which they seem to derive a visible pleasure. When ornamented in this manner they frequently display an almost impish, self-important audacity, strutting about among their companions or advancing upon them in a menacing way. One of the older adults, festooned in this manner, trotted around in a circle with several of the smaller animals following closely behind at her heels. Sometimes the entire company playing in this fashion would march around in a circle, one behind the other, the largest animal stamping its foot violently at each step as though giving the time for the parade. The other animals followed suit by an exaggerated accentuation of the marching movements.

Not only did these apes show many modes of employing objects which they encountered in their environment, but some of them, going a step further, manifested a degree of ingenuity in the construction of implements. The results of this constructive activity, it must be admitted, were relatively simple. On the other hand, it showed a definite tendency on the part of the chimpanzee to combine objects in order to derive from such combinations an even greater utility. Thus, one of the most gifted of these animals ultimately learned to fit a smaller piece of bamboo into a cavity of a larger piece, thus producing for his special purposes a really long bamboo pole which was useful for procuring desired food which had been suspended above his head out of reach. A similar tendency to constructiveness was also observed in certain building propensities ultimately developed by these chimpanzees. When the animal cannot reach an objective hung high above it, it will utilize a box which may be found in the enclosure and thus attempt to decrease the difficulty of space intervening between it and the desired object. There is a possibility also that the chimpanzee may pile two or more boxes, one on top of another, and thus reach his goal. By adequate experiment it was determined that nearly all the animals eventually developed the ability to construct this sort of tower arrangement in order to climb up and get the banana suspended above their heads. The expertness, as well as the efficiency with which the chimpanzee learned to perform this feat, differed considerably in different individuals. The more alert and quickly reacting members of the group accomplished the performance first. The others were slower, aided no doubt, to some extent, by imitation. The quicker chimpanzees actually put this procedure into operation entirely of their own initiative and thus manifested a definite constructional idea. Often, having constructed the tower, a long stick was used in order to gain a nearer approach to the suspended fruit and by means of the stick to bring the fruit to earth. Here two modes of reaction were combined, namely, that of actual building to serve as a basis from which to employ an implement whose uses were already well understood.

These building operations soon became a favorite pastime among the group, but in spite of the fact that the animals were permitted every opportunity to cooperate in their constructive activities, they never fully developed any indication of systematic collaboration. However helpful such combined efforts might have been toward their ultimate aim, the apes failed to utilize the advantages of mutual associations in these transactions. The underlying reason for this apparent deficiency in cooperation may perhaps become clear when it is considered that the obtaining of food among a group of animals, particularly among these chimpanzees, was not in reality a mutual interest. It was from the beginning and always remained a matter of wholly selfish individual acquisition. Whatever division of labor there might be, there never was a thought of dividing the spoils.

When the chimpanzees were assembled in the presence of an objective hung over their heads, they gazed about for proper materials to use as tools to approach their goal. One would bring a pole, another a box. These would be dragged up into position preparatory to constructing a tower. The building would then begin and when the first stages of construction were completed, several of the animals would manifest an assertive disposition to ascend at the same time, and each of them would act as if it alone were the builder. Often, too, the box already in position would be snatched away by some competitive group in the building industry and the pilfered object used in the construction of another independent tower. This would frequently result in a wrangle among the architects; in fact, the entire company of builders might come to blows over this irregularity and infringement of property rights. After the subsidence of such Babel-like controversies, building was resumed and the structure continued to grow in height until it became an object of ever greater excitement to the assembled workers, each manifesting a still keener desire to mount it. As the result of this highly individualistic competition, the object of their main interest tumbled over and was destroyed in the struggle. In consequence, it was necessary to begin the structure all over again and, perhaps, in the continued effort only the more diligent and patient of the group adhered to the original purpose. The others became interested in some less exacting occupations which imposed no actual strain of cooperation upon the individual. Eventually, however, the tower was finished and the more diligent as well as the more tenaciously patient of the animals, without the obtrusive assistance of restless companions, quietly mounted to the summit of the structure, and either with or without the aid of the pole, obtained the coveted food. Sometimes, however, before the diligent one had time to reap the reward of his efforts, some member of the group, endowed with more athletic alertness, stealthily and with great speed, clambered up to the point of vantage to seize the prize with rapacious deftness before the rightful winner had time to protest or retaliate. In all of this cooperative activity there seems to be something so fundamentally human, so reminiscent even of modern acquisitive procedure, that it appears inaccurate to restrict it too rigidly within the category of simian behavior.

The chimpanzee's register of emotion is greater than that of the average human being for the reason that his whole body becomes agitated in such expression; he shows his feelings in other parts of his body than merely his facial muscles. It is his custom to jump up and down in joyful anticipation as well as in impatient annoyance and anger. In extreme despair, which seems to develop as a result of but slight provocation, he flings himself upon his back, rolls wildly to and fro, swings and waves his arms above his head in a fantastic manner, not, Dr. Köhler thinks, unlike the reactions among non-European races as a sign of disappointment and dejection. These anthropoids are not known to weep nor do they laugh in quite the human sense of the term, but there is a certain resemblance to human laughter in the rhythmic gasping and grunting when they are tickled. Probably this manifestation is

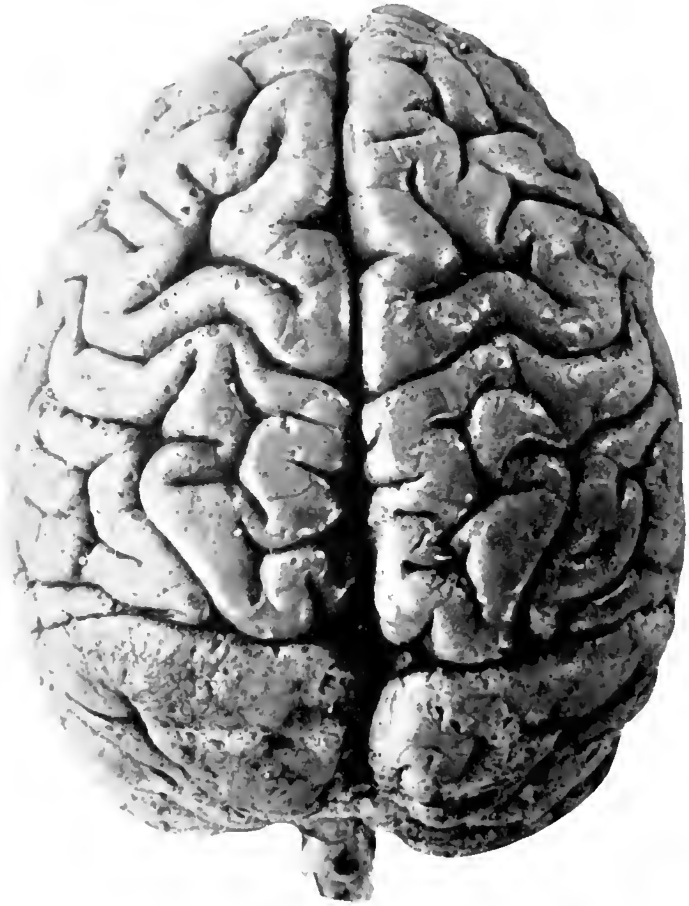


FIG. 251A. DORSAL SURFACE OF BRAIN, CHIMPANZEE.
[Actual Length 96 mm.]

physiologically closely akin to laughter. During the quiet contemplation of objects which seem to give them particular pleasure, and the most conspicuous among such objects are little human children, the entire face of the chimpanzee, especially the outer corners of the mouth, has an expression which is not altogether unlike a human smile. When perplexed, uncertain or in doubt, the chimpanzees have a way of scratching the surface of the body, especially the arms, breast and the upper portion of the thigh. They seem to have a certain degree of understanding among themselves which conveys

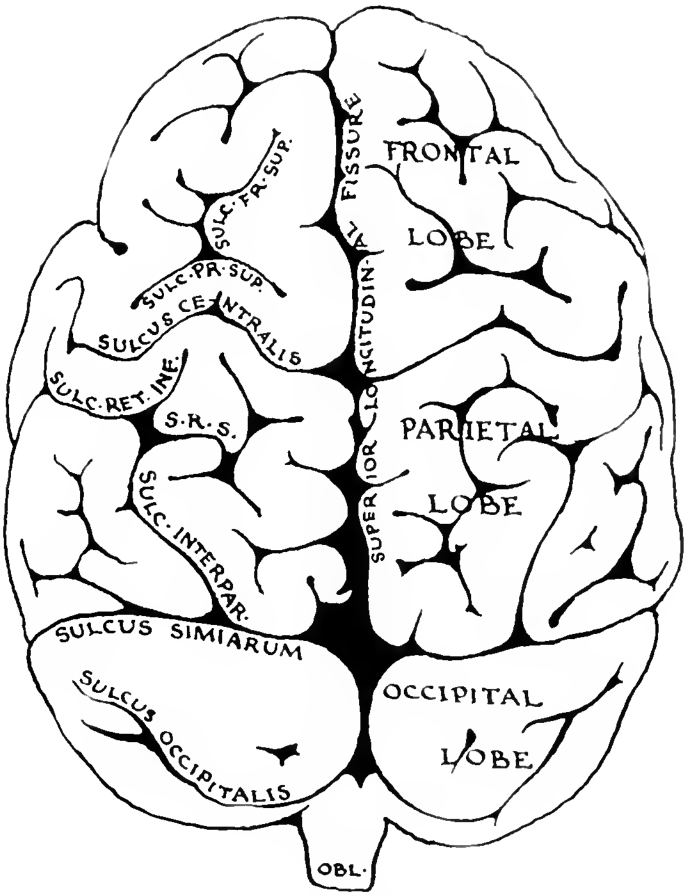


FIG. 251B. DETAILED DIAGRAM OF DORSAL SURFACE OF BRAIN, CHIMPANZEE.

KEY TO DIAGRAM. OBL., Oblongata; SUL. INTERPAR., Sulcus Interparietalis; SULC. FR. SUP., Sulcus Frontalis Superior; SULC. PR. SUP., Sulcus Precentralis Superior; SULC. RET. INF., Sulcus Retrocentralis Inferior, S. R. S., Sulcus Retrocentralis Superior.

the meaning not only of emotional distaste, but also of definite desires and urges whether directed toward another of the same species or toward other creatures or objects.

A large proportion of all their desires is naturally shown by direct imitation of the actions desired. Thus, when one chimpanzee wishes to be accompanied by another, it gives the latter a nudge and pulls it by the hand,

FIG. 252A. BASE OF BRAIN, CHIMPANZEE.

while looking at him and making the movements of walking in the direction of the objective. One wishing to receive bananas from another, imitates the movement of snatching or grasping accompanied by intensely pleading glances. The summoning of another animal from a considerable distance is often accompanied by a beckoning very human in character. The chimpanzee has also a way of beckoning with its foot by thrusting it forward, a little sideways and scratching with it on the ground. Another obvious method of

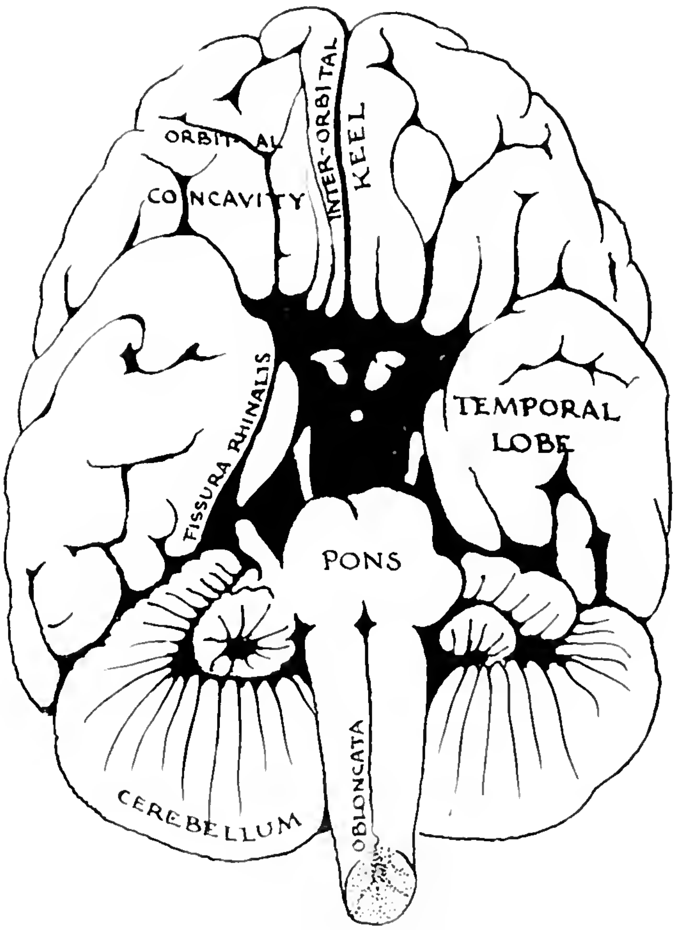


FIG. 252B. DETAILED DIAGRAM OF BASE OF BRAIN, CHIMPANZEE.

invitation is for one ape to indicate in his own person whatever movements he would perform and the activity he wishes the other to undertake, much the same as a dog invites us to play by leaping and running about us. The chimpanzees behave in the same way, inciting others to play with them. In all cases their mimic actions are characteristic enough to be distinctly understood by their comrades. The chimpanzee is especially prone to pay close attention to the wounds or injuries received by his fellows. The incentive in this connection can scarcely be considered as mutual aid. They especially like to remove splinters from each other's hands or feet, employing in this process the methods usually in vogue among the human laity. Two fingernails are pressed on either side of the splinter which is thus elevated until it may be caught and removed by the teeth. Professor Köhler, having suffered from such an accident, ventured to allow one of the chimpanzees to remove the splinter. On perceiving the condition the chimpanzee's expression at once assumed the appearance of eager intensity and his attention was entirely concentrated in preparation for his surgical undertaking. He examined the wound, seized the injured hand, forced out the splinter with two skillful, somewhat powerful squeezes of his fingernails, and then examined the hand closely to be satisfied that his work was well done.

Only a very small portion of Professor Köhler's extensive observations and excellent record during his long experience with these interesting anthropoids has been given here. Those who may be more interested in this subject are referred to his admirable thesis which now has appeared in an English translation entitled "The Mentality of Apes."

The ostensible conclusions as the result of studying this company of nine chimpanzees under the most favorable circumstances may be summarized as follows: The chimpanzee manifests intelligent behavior of a general kind familiar in human beings. Not all of their intelligent acts are externally similar to human acts, but under well-chosen experimental conditions the type of intelligent conduct can always be traced. This applies in spite of very important differences between one animal and another, even to the least gifted specimens of the species that have been observed, and therefore must hold good for every member of the species as long as it is not mentally deficient in the pathological sense of the word. With this exception, which is presumably rare, the success of intelligence tests in general will be more likely endangered by the person making the experiments than by the animal. One must know, and if necessary establish by preliminary observation, within which limits of difficulty and which functions the chimpanzee cannot possibly show intelligence and insight. Negative or confused results from complicated and accidentally chosen test material have obviously no bearing upon the fundamental question, and in general experimenters should recognize that every intelligence test is a test not only of the creature examined but also of the experimenter himself.

In any event, it remains true that chimpanzees not only stand out against the rest of the animal world by several morphological and, in its narrower sense, physiological characteristics, but they also behave in a way which counts as specifically human. As yet we know little of their neighbors of the other side among the anthropoids; but according to the little we do know, with the results of this report, it is not impossible that in this region of experimental research the anthropoid may be found nearer to man in intelligence than to many of the lower species of apes. So far observations agree well with the theory of evolution, and in particular, the correlation between intelligence and the development of the brain is confirmed.

Studies Other than Köhler's upon the Chimpanzee

Other chimpanzees have been studied from time to time with almost similar results and conclusions. One further detail adding to the intelligence tests applied to these animals was made some years ago by Romanes upon the chimpanzee, Sally, which, under his tutelage and instruction, developed the ability to count. In any event, this animal could distinguish a number of straws to six or seven and upon request would indicate with the straws the exact number she had been instructed to show. These facts, in combination with the many exhibition performances which show a striking human resemblance in their execution, would seem to indicate a wide range of teachability on the part of the chimpanzee. Whether such exhibition performances of the animal as are the result of training may be accounted as properly within the definition of strict intelligence tests, is a question somewhat aside from the point. All of these feats of learning, however interpreted, manifest the degree to which the chimpanzee is able to expand its behavioral performances. That the execution of such acts requires appropriate supervision and urging is certainly true, since the animal tends to relapse into more primitive modes of reaction, without apparently having gained any definite advantage for its own purposes of life from the many additional accomplishments acquired under the tutelage of man.

Brain Measurements and Indices in Chimpanzee

The dimensions of the brain, including cerebellum and brain stem, are:

Longitudinal	100 mm.
Transverse	88 mm.

The following are the dimensions of the brain case:

Total length of the skull	190 mm.
Occipito-nasal length	149 mm.
Intertemporal width	72 mm.
Width of the brain case	99 mm.

The total weight of the brain without the dura mater is 350 gm.

Total water displacement	369 c.c.
Weight of the forebrain	298 gm.
Weight of the midbrain	5 gm.
Weight of the hindbrain	47 gm.

The indices as computed on this basis are:

Forebrain index, displaces 310 c.c	83 per cent
Midbrain index, displaces 4 c.c.	5 per cent
Hindbrain index, displaces 55 c.c	12 per cent

A forebrain index of 83 per cent (by weight) assigns this animal to the distinctly manual group, an estimation which accords well with the actual behavior of the chimpanzee.

Surface Appearance of the Brain in Chimpanzee

The pattern and appearance of the cerebral hemisphere in the chimpanzee may be said to be that of a human brain in miniature. With a few notable exceptions, the convolutional design of this anthropoid corresponds closely to that of man, and might easily be mistaken for the latter were it not for its diminutive size, actually being about one-quarter the volume of the human brain. The characterization of the chimpanzee's hemisphere as a human miniature applies equally to the other two great anthropoid apes. The chimpanzee, however, does retain marks of its inherent primitiveness which are considerably more pronounced than in the case of the gorilla, although less defined than in the orang. A careful comparison of all the markings on the surfaces of the endbrain and the brain stem would almost certainly place the chimpanzee below the gorilla and somewhat above the orang-outang.

FISSURES AND LOBES

The fissural pattern on the lateral surface of the hemisphere is anthropoid in type, as determined by the presence of three principal fissures, namely, the fissure of Sylvius whose long horizontal limb has less of the usual simian obliquity, the central fissure of Rolando which divides the lateral surface into two nearly equal areas and presents an upper and a lower genu, and the marked sulcus simiarum which is continuous on the mesial surface with the sulcus in the human brain known as the parieto-

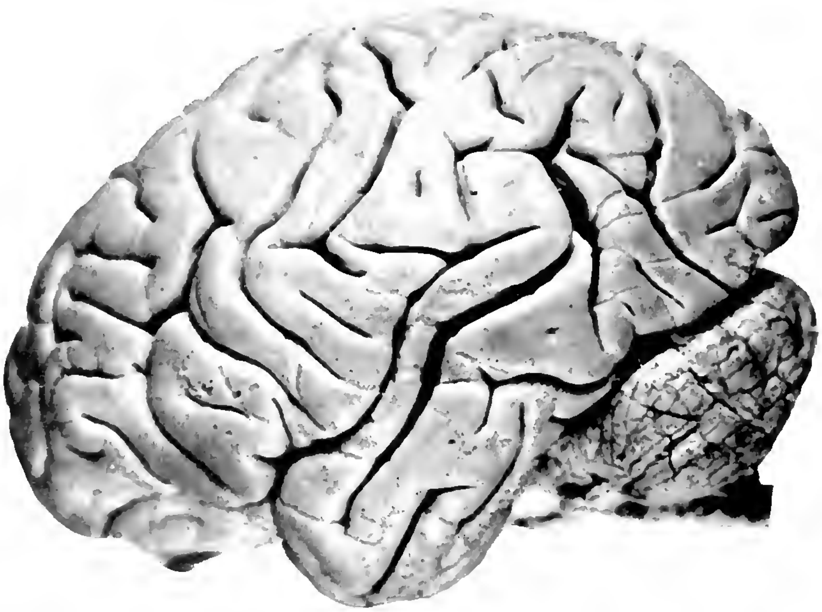


FIG. 253A. LEFT LATERAL SURFACE OF BRAIN, CHIMPANZEE.
[Actual Length 100 mm.]

occipital fissure. These fissures separate the frontal from the parietal, the parietal from the temporal and the parietal from the occipital lobes, thus establishing definite boundaries for a distinct lobational design on the lateral surface of the hemisphere. As is the case with all of the great apes, the richest convolution appears in the parietal area, or somesthetic region of the brain, within which the syntheses of body sensation are elaborated. The convolutional pattern of the frontal lobe is also rich, although considerably less than in man. All of the frontal convolutions of the human brain may be discerned; some of them, however, only incompletely outlined by secondary frontal fissures. The complexity of convolutional design in the brain of chimpanzee compares favorably with human specimens showing a low degree of organization. The temporal lobe has convolutions and fissures characteristic of the human brain. These fissures assume their typical posi-

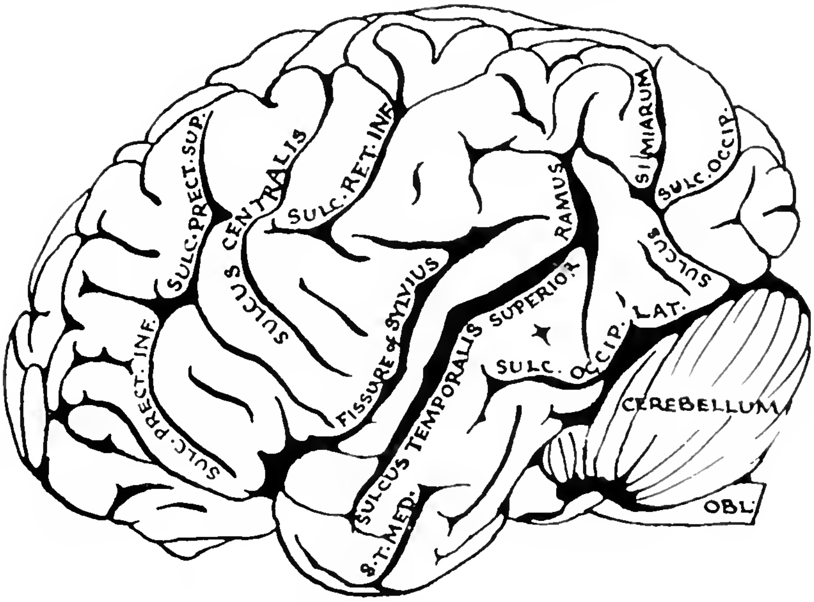


FIG. 253B. DETAILED DIAGRAM OF LEFT LATERAL SURFACE OF BRAIN, CHIMPANZEE.

KEY TO DIAGRAM. OBL., Oblongata; RAMUS, Ramus Posterior of Sulcus Temporalis Superior; SULC. OCCIP., Sulcus Occipitalis; SULC. OCCIP. LAT., Sulcus Occipitalis Lateralis; SULC. PRECT. INF., Sulcus Precentralis Inferior; SULC. PRECT. SUP., Sulcus Precentralis Superior; SULC. RET. INF., Sulcus Retrocentralis Inferior; S. T. MED., Sulcus Temporalis Medius.

tions with a general tendency to extend into the parietal lobe. The sulcus simiarum is somewhat longer than in gorilla, coming well down behind the caudal extremity of the temporal lobe.

The convolutional design on the lateral surface of the occipital lobe is notably feeble. Only a few of the secondary fissures make their appearance in this region. On the mesial surface, however, the cuneus shows somewhat greater complexity in its convolutional pattern even than the human brain. This is due to the fact that a deep annectent gyre in the upper extremity of the simian fissure comes to the surface and thus interrupts the continuity of this fissure with the occipito-parietal fissure. In the human brain, this deep annectent gyre is submerged and thus permits the occipito-parietal sulcus to give the appearance of continuity in which its parietal portion incises the lateral surface. This apparent independence of the two divisions of the parieto-occipital sulcus in the chimpanzee affords some ground to doubt the actual homology with the parieto-occipital fissure in man. It also seems to offer a reason for questioning whether the sulcus simiarum has a representative vestige in the human brain.

THE BASAL SURFACE OF THE HEMISPHERE

Upon the basal surface of the hemisphere, certain characteristic markings indicate that the brain of the chimpanzee is more primitive than that of the gorilla. Thus the orbital concavity, into which the orbital portion of the frontal bone extends, is a particularly marked feature. This concavity indicates a failure on the part of the frontal lobe to expand at the expense of the orbit. The olfactory bulb and tract are detachable as far back as the trigonum olfactorium, and a well-defined gyrus rectus is demarcated by the presence of an olfactory sulcus. The angulation at the chiasm, both with the optic nerves and the optic tracts, is characteristic of all other simian forms, tending to be obtuse rather than acute as it is in most of the lower mammals. The uncus is present on the mesial surface of the temporal lobe, and, although well defined, is less prominent than in gorilla. The cerebellar concavity in the occipital region is more prominent than it is in the gorilla, particularly that portion of it which constitutes the postsplenial fossa, into which projects the highly elevated cephalic portion of the superior vermis of the cerebellum. In all of its features on the basal surface of the hemisphere the brain of the chimpanzee approaches more closely that of the intermediate primates than of man, and appears to be less advanced in this direction than the brain of gorilla as judged by these crucial points of basal identification.

THE CEREBELLUM

The cerebellum presents its usual divisions and surfaces. The tentorial surface is distinctly more gabled than is the case of gorilla, though somewhat less than in the baboon or macacus. The superior vermis appears as a definite ridge-pole and is particularly pronounced at its cephalic extremity, which impresses itself upon the undersurface of the hemisphere in the postsplenial fossa. The cerebellar folia pass without interruption from the tentorial surface of the vermis to the tentorial surface of the lateral lobes. These latter structures are less extensive than in gorilla. The posterior notch of the cerebellum is present but has not attained the depth characteristic of man. Upon the occipital surface the inferior vermis is still a notable feature. It has not been so much submerged by the expansion of the lateral lobes as in the case of the human and gorilla brains. It is separated from the lateral cerebellar expansions by two vermolateral sulci which somewhat interrupt the passage of the fissures from the median portion to the lateral lobes. The petroso-ventricular surface of the cerebellum shows little that is distinctive in chimpanzee. The ventricular portion occupies a position in relation to the roof of the fourth ventricle. The superior vermis in this region projects much higher than in the case of either man or gorilla. The petrosal portion is occupied by the cerebello-pontile angle in which is lodged a flocculus which is relatively small. As a whole, the cerebellum, both in form and dimensions, appears to be intermediate between that of man and gorilla on the one hand, and the intermediate primates on the other.

THE BRAIN STEM

The Oblongata. The markings on the brain stem in the chimpanzee are, if anything, somewhat less defined than might be expected from the prominence of the landmarks of the hemispheres. The oblongata upon its ventral surface presents two well-defined pyramids separated by a ventromedian sulcus. At the caudal extremity of the pyramid interlacing fibers of the decussation may be discerned upon the surface. Lateral to the pyramid,

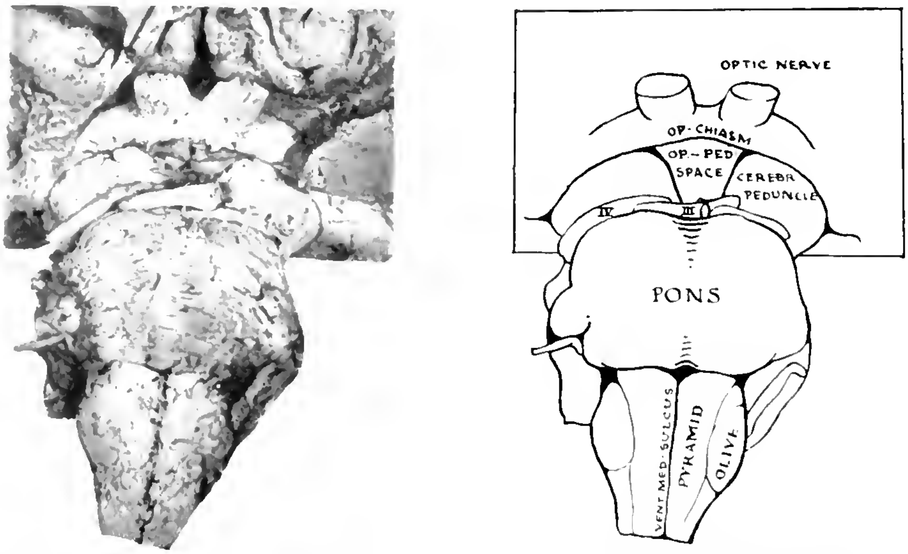


FIG. 254. VENTRAL SURFACE OF THE BRAIN STEM, CHIMPANZEE.
[Actual Length 48 mm.]

KEY TO DIAGRAM. CEREBR. PEDUNCLE, Cerebellar Peduncle; OP- CHIASM, Optic Chiasm; OP. PED. SPACE, Opticopeduncular Space; VENT. MED. SULCUS, Ventromedian Sulcus.

and separated from it by the preolivary sulcus, is a well-defined olivary eminence, which in turn is separated from the tuberculum trigemini by the postolivary sulcus. The dorsal surface of the oblongata presents the two characteristic divisions, the infraventricular and the ventricular portion. The infraventricular portion is characterized by the appearance of a well-defined dorsomedian septum, on either side of which may be seen the elevations produced by the fibers and nucleus constituting the clava. The usual dorsal paramedian sulcus separates the clava from the cuneus, which latter appears to be the larger of these two surface elevations. From this fact it may be inferred that the sensory importance of this area has increased, due to the specialization of the upper extremity and hand. The influx of sensory stimuli is undoubtedly greater from this part of the body than from the lower extremity. A greater degree of specialization is manifest in the hand,

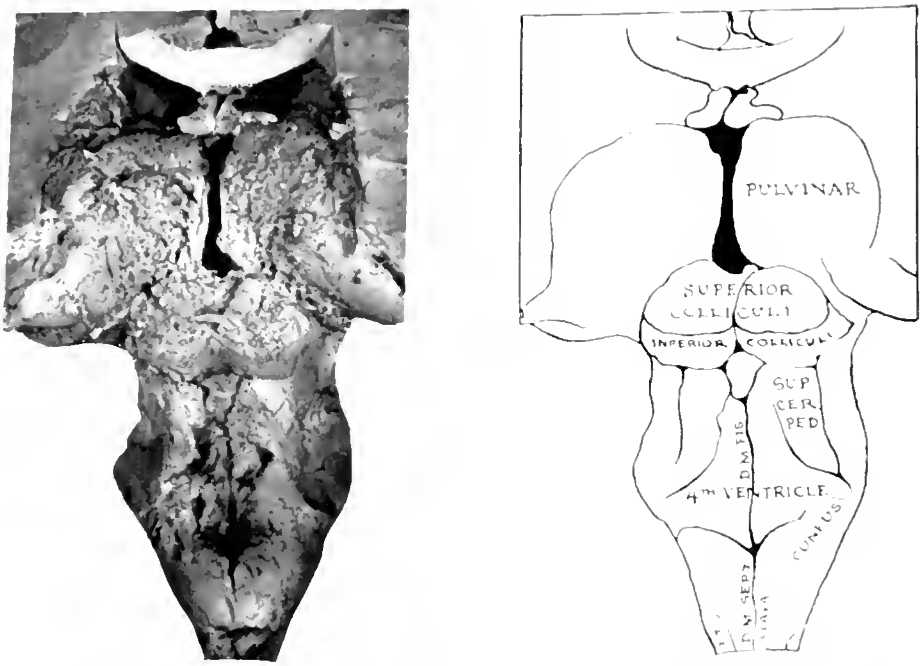


FIG. 255. DORSAL SURFACE OF BRAIN STEM, CHIMPANZEE.
[Actual Length 48 mm.]
KEY TO DIAGRAM. D. M. FIS., Dorsomedian Fissure; D. M. SEPT., Dorsomedian Septum; SUP. CER. PED., Superior Cerebellar Peduncle; T. T., Tuberculum Trigemini.

forearm and arm than in the leg. Taking into account its relation both to locomotion and to the many feats of manual dexterity of which the chimpanzee is capable, the hand seems to fill a more important office than the foot.

In the ventricular portion of the dorsal surface of the oblongata, the characteristic divergence occurs in the alar plates, thus disclosing the floor of the ventricle. The lateral walls of this inferior angle of the fourth ventricle are formed as elsewhere by the eminences of the clava and cuneus. The clava does not extend as far cephalad as does the cuneus. Both of these eminences decrease in elevation as the lateral recess is approached and at this point have reached the plane of the ventricular floor. It is in this region that the incoming fibers of the acoustic division of the eighth nerve enter the ventricle whose floor they cross as the striae acusticae. The floor of the ventricle contains the trigonum hypoglossi beneath which is located the nucleus of the twelfth cranial nerve and lateral to which is the fovea vagi marking the position of the dorsal vagal nucleus. Other markings in this region are extremely difficult to discern. Two faint elevations appear in the ventricular floor in the region of the lateral recess indicating the position of the vestibular nuclei. As compared with some of the more definitely arboreal forms of primates, these elevations are not so pronounced, but still show a degree of prominence which indicates a balancing mechanism in chimpanzee charged with large responsibilities in the general organization of the animal's motor activity. The cephalic angle of the fourth ventricle, aside from the elevation marking the presence of the nucleus abducentis, and the gradual decrease in its diameters as the ventricle approaches the caudal orifice of the Sylvian aqueduct, shows no particularly outstanding feature. The lateral walls are formed by the middle and superior cerebellar peduncles. In general, the markings of the oblongata, both upon its ventral and dorsal surfaces and in the region of the ventricle, are much less striking than is the case in man or even in the gorilla. The markings are somewhat more clearly defined than in the intermediate primates.

The Pons Varolii. At the cephalic limit of the oblongata upon its ventral surface appears the bulbopontile sulcus which separates the bulb from the pons Varolii. This structure is a fairly pronounced feature of the brain stem in chimpanzee. It does not, however, attain the proportions which are characteristic of it in man or in gorilla. Its lateral extremities are continued to form the middle cerebellar peduncle which approaches and enters the cerebellum to form ultimate connections with the lateral lobes of this organ. The roots of the trigeminal nerve come into relation with the pons Varolii at the point of transition between it and the middle cerebellar peduncle. These fibers penetrate the pontile strata and make their way to the tegmentum of the axis. The cephalic extremity of the pons is marked by a well defined ponto-peduncular sulcus separating the pons Varolii from the cerebral peduncle. In the midline this point of separation is further emphasized by the extension beneath the pons of the blind ending of the optico-peduncular space, the foramen caecum anticum.

THE MIDBRAIN. The midbrain presents upon its dorsal surface the usual specialization of the quadrigeminal plate. This consists of two sets of colliculi corresponding to the structures already observed in all primates in relation to the sense of hearing and the sense of sight. The inferior colliculi are less prominent than the superior colliculi, and both have undergone an appreciable decrease in their elevation above the roof of the midbrain. Longitudinally, the intercollicular sulcus at its cephalic extremity becomes expanded to form the pineal fossa, and it is particularly in this region that the superior colliculi show their greatest attenuation. Judged by these marks of identification it seems clear that the chimpanzee is less well equipped in the mechanism by means of which it executes those immediate reflex reactions in response to the stimuli of hearing, and that the process of telencephalization has advanced much further than in the intermediate primates.

The lateral surface of the midbrain presents the elevation of the mesial geniculate body which may be seen connected with the inferior colliculus by means of a fairly well-defined brachium conjunctivum posticum. The ventral surface of the midbrain is characterized by the appearance of the optico-peduncular space, upon either side of which the cerebral peduncle is diverging to enter the hemisphere. The cephalic boundary of this space is formed by the diverging optic tracts and the optic chiasm. The space contains, as in all other forms, the point of emergence of the oculomotor nerve, the mammillary bodies, the attachment of the infundibular stalk and the tuber cinereum. There are no especially characteristic features in it to distinguish this region from that of other primates.

Internal Structure of the Brain Stem in Chimpanzee

Level of the Pyramidal Decussation (Fig. 256)

At this level the section shows as its most conspicuous feature the decussating fibers of the pyramidal system (Pyx). Occupying the usual ventromesial portion of the section are the still uncrossed pyramidal fibers (Py). The crossing fibers, however, have caused a deflection of the sulcus, and in the course of their decussation have gone so far toward occupying their ultimate position in the spinal cord as to have more or less completely detached the ventral gray column (Ven) from the central gray matter (Cen). On the periphery of the section certain indentures indicate the position of the major sulci on the surface of the stem. The ventromedian sulcus has already been referred to and the deflection in it caused by the decussating pyramidal bundles. A faintly marked intermediate sulcus lies ventral to the substantia gelatinosa trigemini (NR), while dorsal to this structure is the dorsolateral sulcus and a faintly indicated dorsal paramedian sulcus. In the dorsal sensory field, the columns of Goll and Burdach are clearly demarcated by a dorsal paramedian sulcus, the division between the two columns showing clearly a preponderance in size which favors Burdach's column (CB). In the column of Goll (CG) the caudal extremity of this nucleus may be discerned (NG). It is adjacent to the median septum but invested by a dense capsule of myelinized fibers. Extending dorsolaterally from the central gray matter is the proximal portion of the nucleus of Burdach passing outward into the surrounding medullary substance of the corresponding column. A tenuous extension of the central gray connects with the somewhat expanded substantia gelatinosa trigemini (NR) upon whose outer margin are the collected fibers forming the descending trigeminal tract (Trd).

The impression conveyed by a critical survey of this dorsal field with

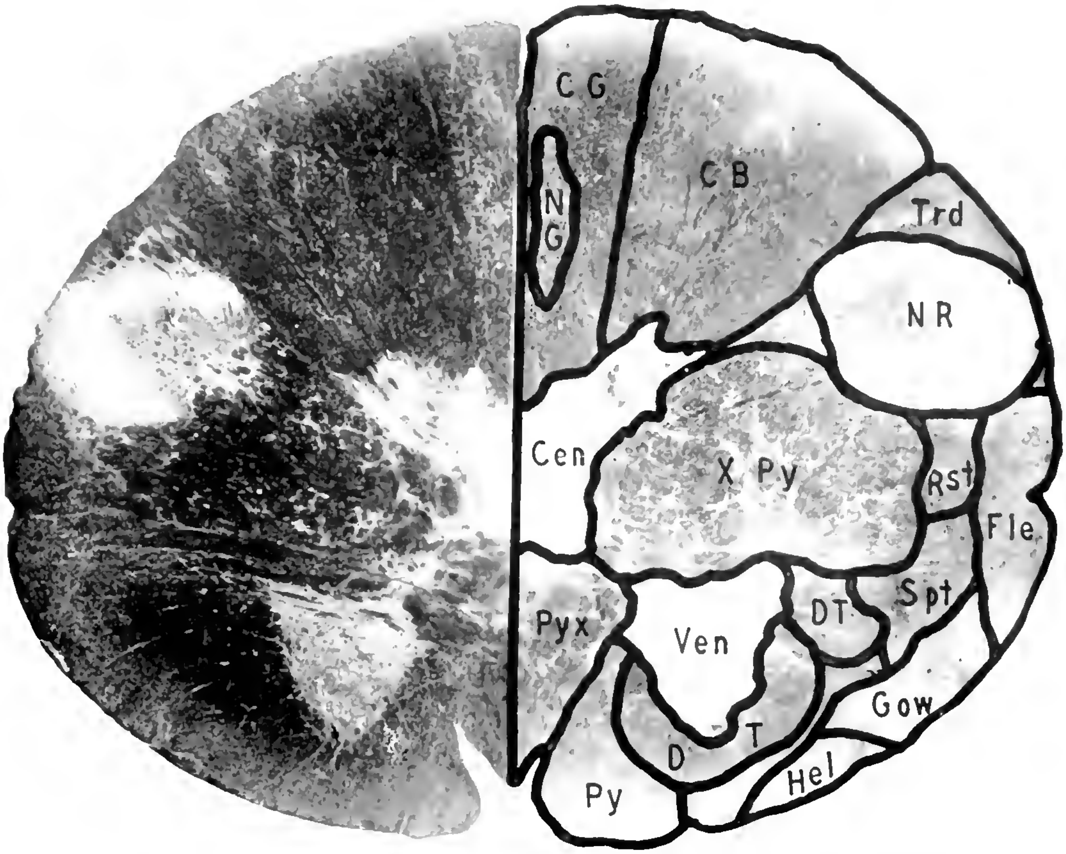


FIG. 256. CHIMPANZEE. LEVEL OF THE PYRAMIDAL DECUSSATION.
CB, Column of Burdach; CEN, Central Gray Matter; CG, Column of Goll; DT, Deitersospinal Tract; FLE, Dorsal Spinocerebellar Tract; GOW, Ventral Spinocerebellar Tract; HEL, Spino-olivary Tract of Helweg; NG, Nucleus of Goll; NR, Nucleus of Rolando; PY, Pyramid; PYX, Pyramidal Decussation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; TRD, Descending Trigeminal Tract; VEN, Ventral Gray Column; XPY, Crossed Pyramidal Tract. [Accession No. 157. Section 50. Actual Size 12 × 9 mm.]

reference to the discriminative capacity of the animal is that of a sensory organization in which the forelimb and hand contribute a greater volume of afferent influx than either the head or the lower extremity. This in the main is the formula for all of the great anthropoids including man, in all of which the column of Burdach is greater than the column of Goll. The formula representing this relation in some lower primates shows the column of Goll to be greater than that of Burdach. The significance of this inversion of sensory relation arises from the growing prominence of manual differentiation seen in the greater anthropoids as well as from the decline of the sensory representation in the caudal portion of the animal, more particularly the tail. The circumferential zone in the chimpanzee has a considerable depth and contains the two ascending spinocerebellar tracts (Fle, Gow). The intermediate zone contains the rubrospinal and spinothalamic tracts (Rst, Spt) and merges insensibly with the reticular formation whose appearance at this level is somewhat diffuse. Neither the central gray matter (Cen) nor the ventral gray column (Ven) presents any marked specialization, although the latter stands out conspicuously because of its detachment in consequence of the heavy decussations of pyramidal fibers (Pyx).

LEVEL OF CAUDAL EXTREMITY OF INFERIOR OLIVE (FIG. 257)

Here the appearance of the section has undergone some change principally because of a considerable increase in all of its diameters. This is occasioned both by the expansion of the dorsal sensory nuclei (NG, NB) and the appearance of a new gray element, the inferior olivary nucleus (IO) whose caudal tip lies immediately lateral to the pyramid (Py). The central gray matter (Cen) is more conspicuous because of its dorsal migration into the position which it will occupy in the floor of the fourth ventricle. Contained in its center is a small central canal. It differs in its appearance from all of the lower levels because of its complete detachment, due to the interposition of internal arcuate fibers arising in the nucleus of Goll (NG). These fibers also detach the central gray matter from the nucleus of Burdach (NB) and the substantia gelatinosa trigemini (NR).

The most pronounced changes occur in the dorsal field and may be ascribed to the expansion of the dorsal sensory nuclei. The nucleus of Goll (NG) has considerably increased in size and is still surrounded by

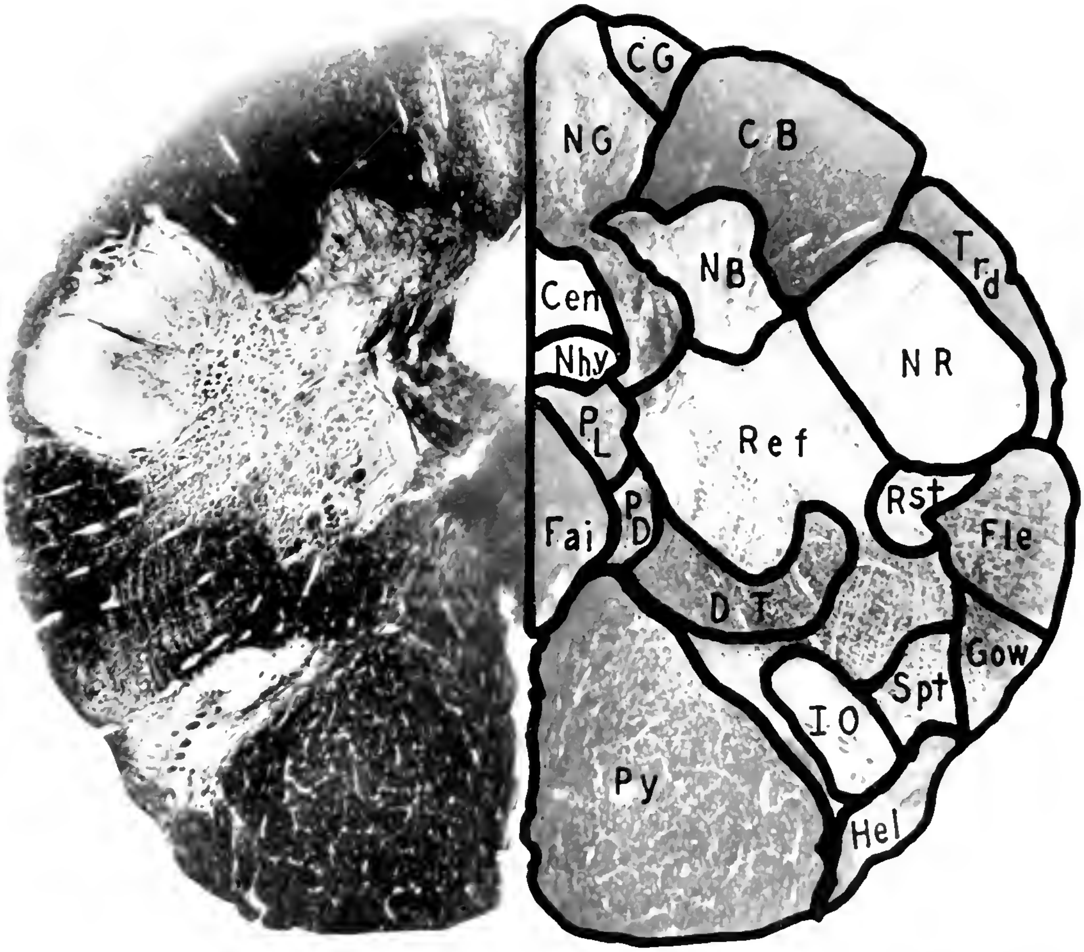


FIG. 257. CHIMPANZEE. LEVEL OF CAUDAL EXTREMITY OF INFERIOR OLIVE.

CB, Column of Burdach; CEN, Central Gray Matter; CG, Column of Goll; DT, Deiterso-spinal Tract; FAI, Internal Arcuate Fibers; FLE, Dorsal Spinocerebellar Tract; GOW, Ventral Spinocerebellar Tract; HEL, Spino-olivary Tract of Helweg; IO, Inferior Olive; NB, Nucleus of Burdach; NG, Nucleus of Goll; NHY, Hypoglossal Nucleus; NR, Nucleus of Rolando; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PY, Pyramid; REF, Reticular Formation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; TRD, Descending Trigeminal Tract. [Accession No. 157. Section 82. Actual Size 13 × 10 mm.]

medullary substance constituting the column of Goll (CG). Neither at this level nor at any lower level is there evidence of the unpaired median nucleus of Bischoff. This fact adds substantiation to the theory already advanced that the nucleus of Bischoff is a functional response to the development of a tail, particularly in such forms as specialize this caudal appendage as a prehensile, supporting or locomotor organ. In general, the nucleus of Goll presents a more disseminated and scattered appearance than is the case with the lower or intermediate primates. In fact the solidarity of Goll's nucleus in most of these lower forms is one of its distinguishing characteristics. The nucleus of Burdach (NB) has not attained its full dimensions. It does, however, appear as a more compact nucleus than that of Goll and is surrounded by a dense field of myelinized fibers forming the column of Burdach (CB). Lateral to the column of Burdach is a large nucleus of Rolando, or substantia gelatinosa trigemini (NR), whose outer margin is in contact with a well-marked descending trigeminal tract (Trd). The substantia gelatinosa trigemini is in continuity with the remnant of the ventral gray column which now presents an indefinite outline and appears to be merging with the reticular formation (Ref).

Dorsal to the pyramid (Py), situated along the median raphe, are the collected axons arising from the internal arcuate fibers (Fai) which form the mesial fillet. The apparent increase in density of this fasciculus implies a certain degree of increment in this central pathway for the conveyance of impulses of discriminative sensibility.

LEVEL THROUGH THE MIDDLE OF THE INFERIOR OLIVE (FIG. 258)

At this level the most pronounced change is determined by the appearance of a large convoluted structure constituting the inferior olivary nucleus (IO). This structure, situated dorsolateral to the pyramid (Py), has in association with it the mesial and dorsal accessory olives (DO, VO).

The surface demarcations of the olive are well shown by the presence of a marked preolivary sulcus. The inferior olive itself has increased in prominence, not only due to increments in its actual cell-containing substance, but

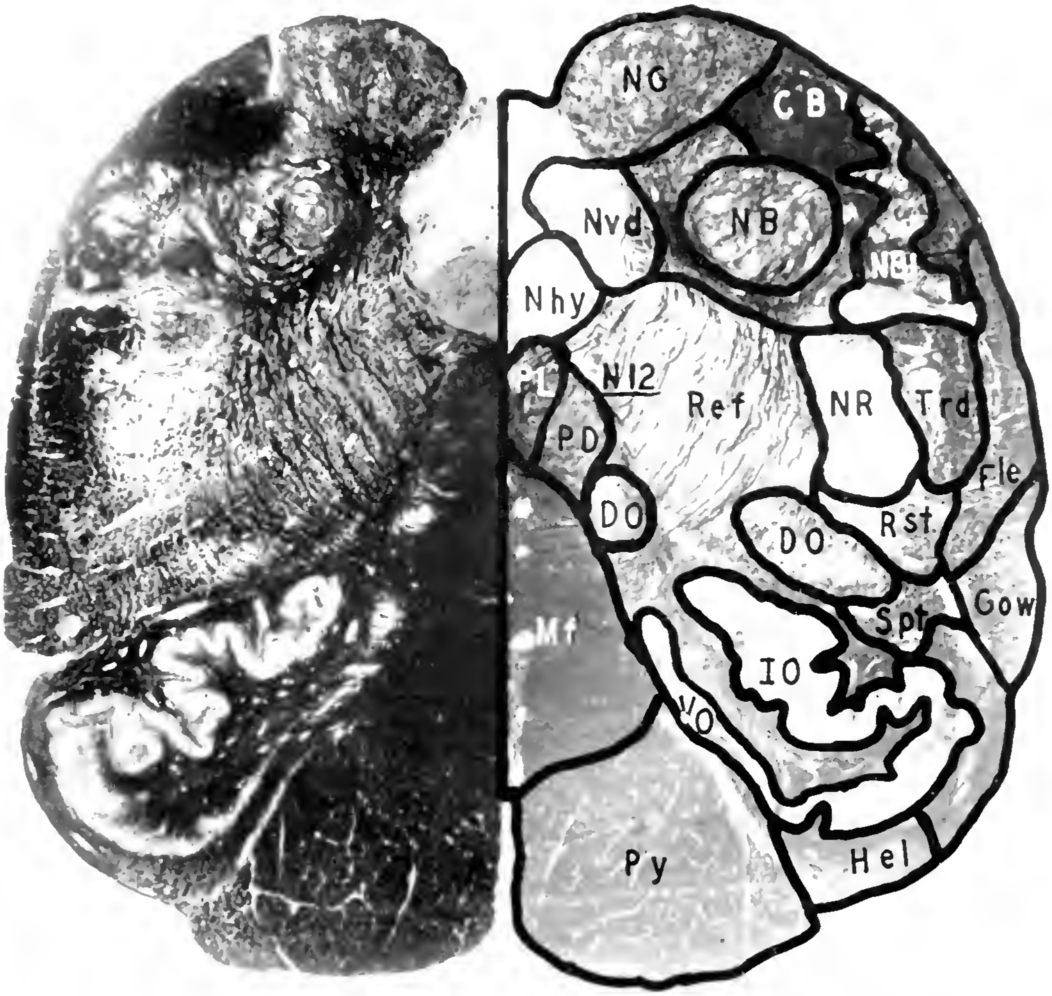


FIG. 258. CHIMPANZEE. LEVEL THROUGH THE MIDDLE OF THE INFERIOR OLIVE. CB, Column of Burdach; DO, Dorsal Accessory Olive; FLE, Dorsal Spinocerebellar Tract; GOW, Ventral Spinocerebellar Tract; HEL, Spino-olivary Tract of Helweg; IO, Inferior Olive; MF, Mesial Fillet; NB, Nucleus of Burdach; NBL, Nucleus of Blumenau; NG, Nucleus of Goll; NHY, Hypoglossal Nucleus; NR, Nucleus of Rolando; NVD, Dorsal Vagal Nucleus; N12, Hypoglossal Nerve; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PY, Pyramid; REF, Reticular Formation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; TRD, Descending Trigeminal Tract; VO, Ventral Accessory Olive. Accession No. 157, Section 150, Actual Size 15 × 12 mm.]

by expansion of its fundus which contains a greater volume of myelinized fibers than in the lower or intermediate primates. The most conspicuous features of the olive in the chimpanzee are its decisive boundary line and definition, together with a marked degree of convolution into which its retaining wall of gray matter is thrown. These particulars correspond closely to those of the structure in the human brain, and are in accord with the functional interpretation given of the inferior olive in this discussion. The advances in olivary organization signify a definite increase in the coordination of simultaneous movements of hands, head and eyes, in the interest of the better performance of skilled acts. The chimpanzee is capable of a remarkable range of performances of this kind, notable because of their great rapidity, precision and force. Animal trainers and scientific observers have alike been impressed by the proficiency and adaptability which this animal manifests in its manual dexterity.

The central gray matter, which has nearly completed its dorsal migration, is about to take up its position in the floor of the fourth ventricle. In its more ventral portion is a large, well-defined nuclear aggregation, the nucleus hypoglossus (N hy) from which the emergent fibers of the twelfth nerve (N 12) pass toward the inferior olive. The definition of this nucleus is more prominent than that observed in the lower and intermediate primates. Lateral to the hypoglossal nucleus in the central gray matter is another nuclear collection of lighter color, with less well-defined boundaries, the dorsal nucleus of the vagus (N v d), connected with which are some entering root fibers of the pneumogastric nerve. Lateral to the central gray matter are the three great nuclei of the dorsal sensory field, first the nucleus of Goll (N G), second, the nucleus of Burdach (N B) and third, the nucleus of Rolando (N R). The nucleus of Goll (N G) is considerably smaller than the nucleus of Burdach (N B), which is at least twice the size of either of its sensory neighbors. The nucleus of Burdach shows the typical accessory nucleus of Blumenau (NBl). The nucleus of Rolando (NR) (the substantia gelatinosa trigemini) is considerably less in size than the nucleus of Goll and also less sharply defined in outline. It has in contact with its outer margin the descending trigeminal tract (Trd) across whose outer surface pass many of the fibers of the ascending spinocerebellar system (Fle) entering into the formation of the restiform body. The intermediate fissure, together with the postolivary sulcus, bounds a slight eminence on the lateral surface which corresponds to the position of the more ventral of the two spinocerebellar tracts (Gow) mesial to which are situated the rubrospinal and spinothalamic tracts (Rst, Spt). The reticular formation (Ref) forms the center of the section and is penetrated by many internal arcuate fibers, chiefly those taking origin in the nucleus of Burdach. These make their way inward toward the raphe, where they undergo decussation to enter the mesial fillet (Mf). Ventral to the latter is the compact bundle constituting the pyramid (Py).

LEVEL OF THE VESTIBULAR NUCLEI (FIG. 259)

Here the chief alteration in the section is determined by the wide opening of the fourth ventricle and the appearance, in the position previously occupied by the dorsal sensory nuclei, of the two vestibular nuclei forming the central primary stations of the proprioceptors situated in the semicircular canals, utricle and saccule. The central gray matter here occupies its typical position in the floor of the fourth ventricle and shows certain minor differences from the arrangement of this structure in previous levels. In the first place, it includes the cephalic extremity of the hypoglossal nucleus (Nhy) as its fibers pass forward toward the inferior olive (IO), lateral to which is the cephalic remnant of the dorsal vagal nucleus (Nvd). Interposed between the hypoglossal nucleus and the dorsal nucleus of the vagal nerve is the well-defined nuclear mass constituting the lower extremity of the vestibular nucleus of Schwalbe (NSc). Adjacent and lateral to this triangular nucleus is an area characterized by the presence of small scattered bundles of myelinized fibers in a field of gray matter, the nucleus of Deiters (ND).

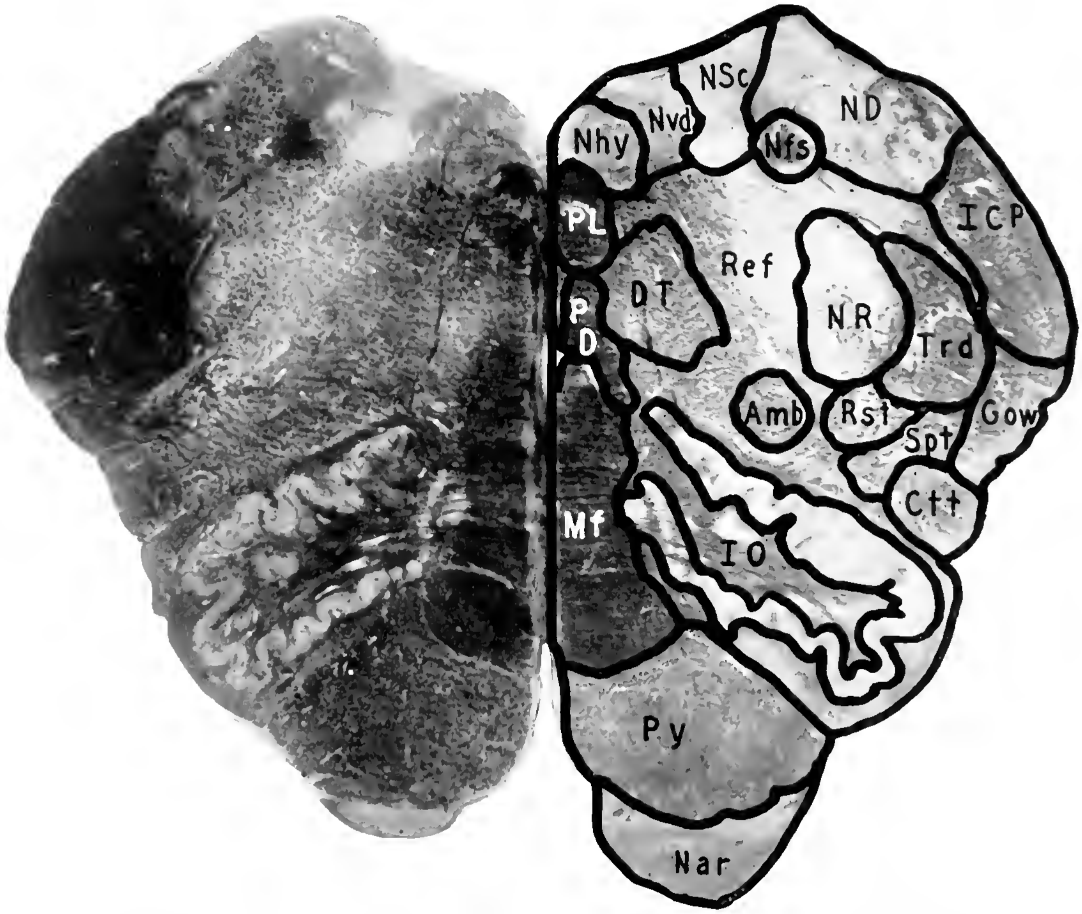


FIG. 259. CHIMPANZEE. LEVEL OF THE VESTIBULAR NUCLEI.

AMB, Nucleus Ambiguus; CTT, Central Tegmental Tract; DT, Deiterso-spinal Tract; GOW, Ventral Spino-cerebellar Tract; ICP, Inferior Cerebellar Peduncle; IO, Inferior Olive; MF, Mesial Fillet; NAR, Nucleus Arciformis; ND, Nucleus of Deiters; NFS, Nucleus Solitarius; NHY, Hypoglossal Nucleus; NR, Nucleus of Rolando; NSC, Nucleus of Schwalbe; NVD, Dorsal Vagal Nucleus; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PY, Pyramid; REF, Reticular Formation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; TRD, Descending Trigeminal Tract. [Accession No. 157. Section 221. Actual Size 18 × 9 mm.]

Many fibers of the vestibular division of the eighth nerve enter this nucleus. Thus, while the central gray matter still presents those specializations characteristic of the hypoglossal and vagal nuclei, this level of the brain stem illustrates with what phyletic constancy the two great nuclei of the vestibular mechanism make their appearance in a topographical position corresponding to that occupied by the nuclei of Goll and Burdach at the lower levels of the axis.

It is not possible from this figure to judge of the dimensions, and consequently the functional prominence of the vestibular complex in the chimpanzee. The appearance of it in reconstruction and its surface relief in the floor of the fourth ventricle indicate that this complex, while somewhat less prominent than in the strictly arboreal primates, is considerably more conspicuous than in man or gorilla. This observation coincides with the motor activities upon which the chimpanzee depends for its great speed in climbing as well as getting about, either upon all fours or in its somewhat awkward upright posture on the ground. Studies of the actions of the chimpanzee in captivity reveal the high degree of balancing specialization which the animal possesses in its many intricate and delicate performances. The relative lightness of its body, as compared to man and the gorilla, permits of a facility in climbing possessed by neither of the other primates mentioned. The adaptation of its feet and arms to locomotion in the trees as well as upon the ground calls for special developments of balancing, which, combined with other necessities in this respect, undoubtedly account for the well-developed central mechanism illustrated by the large size of the vestibular complex.

Ventral to Deiters' nucleus is the now much reduced mass of the substantia gelatinosa trigemini (NR) whose outer margin is in contact with the descending trigeminal tract (Trd). The outer surface of Deiters' nucleus as well as the descending trigeminal tract are covered by a massive bundle of fibers constituting the restiform body (ICP). The intermediate and postolivary sulci still bound the lateral intermediate eminence marking the position of the more ventral of the two spinocerebellar tracts (Gow), mesial to which are the rubrospinal and spinothalamic fasciculi (Rst, Spt). The inferior olive appears perhaps even more conspicuous at this level than in the one previously described. It shows all of its characteristics in convolutions, definition of outline, size of fundus and richness of fiber connections. Mesial to it is the dense bundle constituting the central pathway of discriminative sensibility, the mesial fillet (Mf), while in the ventromesial position of the section is the massive pyramid (Py). A notable addition in connection with the ventral surface of the pyramid is the appearance of a relatively large mass of gray matter, the nucleus arciformis (Nar). This structure appears to be the caudal extension of the nuclear masses which constitute the pontile nuclei. One of the most striking features of the brain stem in the great anthropoids is the increase in the pons Varolii, particularly in its nuclear masses, whose extension below the caudal pontile limits along the ventral surface of the pyramid is expressive of extreme activity in growth. There may be objections to this interpretation of the nucleus arciformis on the ground of its connections. In reconstruction, however, this nucleus appears to be in direct continuity with the gray matter constituting the nuclei of the pons. It appears only in those primates in which the pons Varolii has shown that exuberant expansion which develops in direct consequence of growth in the cerebral hemispheres.

LEVEL OF THE CEREBELLAR NUCLEI (FIGS. 260, 261 AND 262)

At this level the most prominent feature is the appearance of the nucleus dentatus (NDt) which is situated in the medullary vestibule of the cerebellum. At this level also the cerebellum occupies a position above the roof of the fourth ventricle, into the cavity of which projects a portion of the inferior vermis (Ver). The cavity itself is more spacious than in previous sections. The floor of the ventricle is broader than elsewhere because of the presence of the two large lateral recesses, connected with each of which is the dorsolateral eminence which constitutes the tuberculum acusticum. Entering into these eminences are the fibers of the acoustic division of

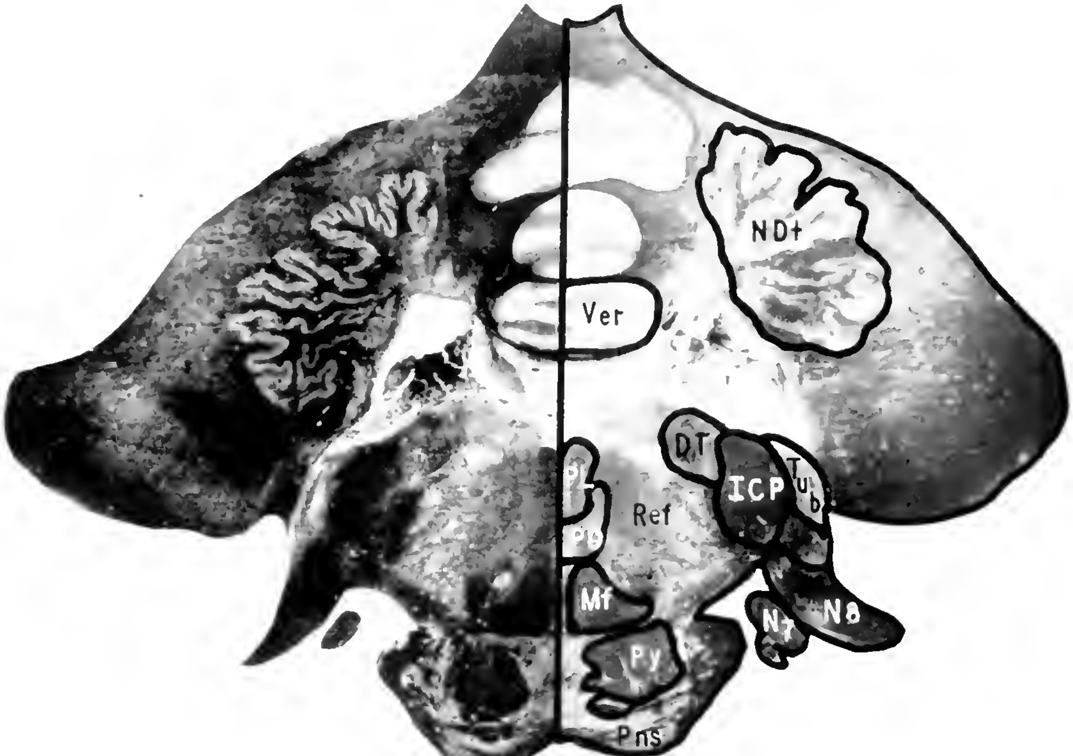


FIG. 260. CHIMPANZEE. LEVEL OF THE CEREBELLAR NUCLEI.

DT, Deiters' Nucleus; ICP, Inferior Cerebellar Peduncle; MF, Mesial Fillet; NDT, Dentate Nucleus; N7, Facial Nerve; N8, Auditory Nerve; PD, Fasciculus Predorsalis; PL, Fasciculus Longitudinalis Posterior; PNS, Pons; PY, Pyramidal Tract; REF, Reticular Formation; TUB, Tuberculum Acusticum; VER, Vermis. [Accession No. 157. Section 270. Actual Size 32 × 23 mm.] Figures 260, 261 and 262 are introduced to illustrate character and extent of the cerebellar nuclei.

the eighth nerve. The appearance of the dentate nucleus (NDT) is of particular interest. Its general outline gives the impression of a definite festooning in the nuclear substance which has assumed the appearance of a thin ribbon of gray matter dipping down in many irregular depressions of considerable length. Each such depression is characterized by lesser undulations in the surface of the gray matter. This appearance of the nucleus is distinctive and has been observed thus far only in the chimpanzee. The characteristic features about it are these deep festoon-like curves which are so

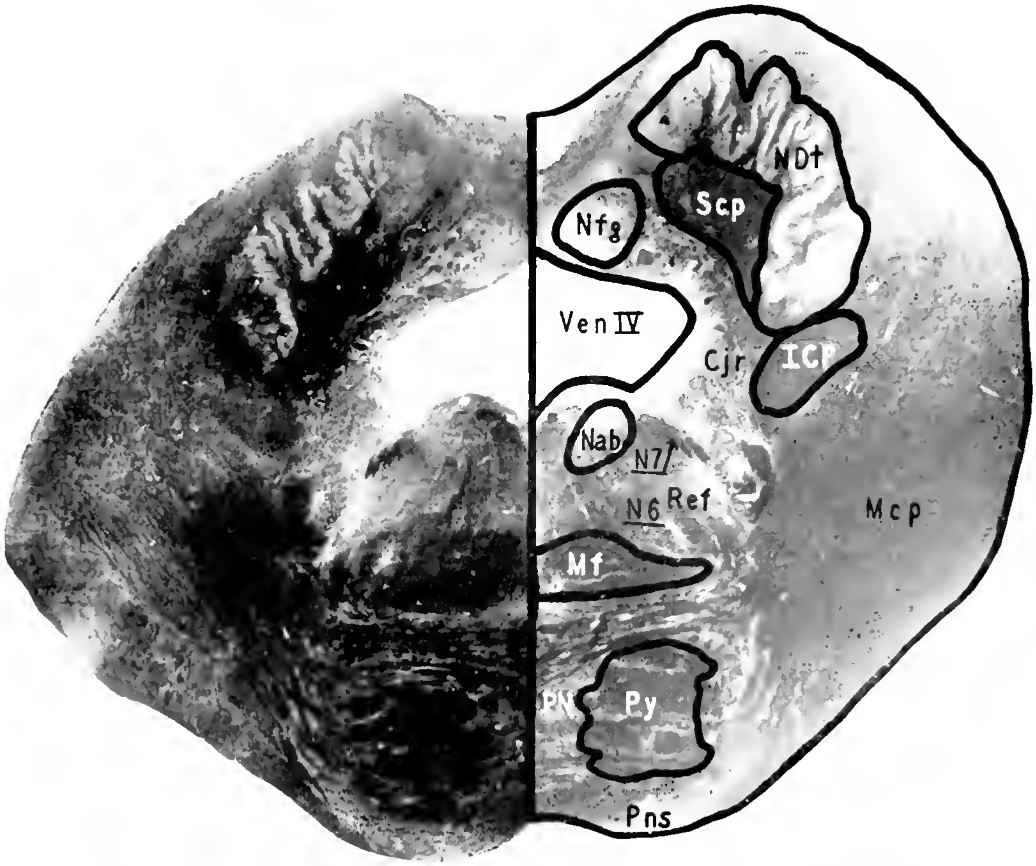


FIG. 261. CHIMPANZEE. LEVEL OF THE CEREBELLAR NUCLEI.

CJR, Corpus Juxtarestiforme; ICP, Inferior Cerebellar Peduncle; MCP, Middle Cerebellar Peduncle; MF, Mesial Fillet; NAB, Nucleus Abducentis; NDT, Nucleus Dentatus; NFG, Nucleus Fastigii; N6, Abducens Nerve; N7, Facial Nerve; PN, Pontile Nuclei; PNS, Pons; PY, Pyramidal Tract; REF, Reticular Formation; SCP, Superior Cerebellar Peduncle; VEN IV, Fourth Ventricle. [Accession No. 157. Section 240. Actual Size 38 × 26 mm.]

extensive as almost to isolate portions of the nucleus from the main mass of the structure. In its most primitive condition the dentate nucleus has a far simpler outline with little or no tendency to convolution and imperfect sacculation. In its highest morphological development it appears preeminently as a saccular structure with some resemblance to the inferior olivary body. The degree of convolution in the wall of the dentate nucleus varies considerably as the result of the complexity of its organization. In all

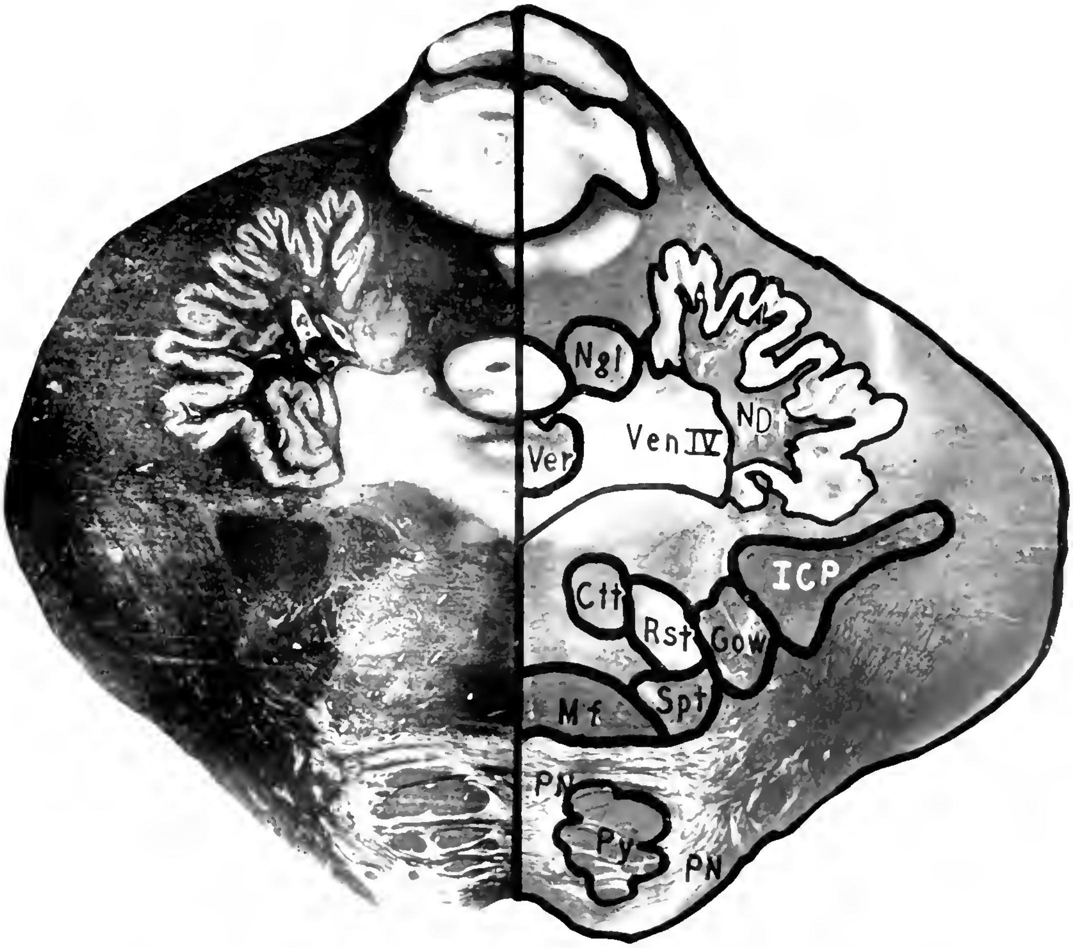


FIG. 262. CHIMPANZEE. LEVEL OF THE CEREBELLAR NUCLEI.

CTT, Central Tegmental Tract; GOW, Ventral Spinocerebellar Tract; ICP, Inferior Cerebellar Peduncle, MF, Mesial Fillet; NDT, Cerebellar Nuclei, Lateral Group; NGT, Cerebellar Nuclei, Mesial Group; PN, Pontile Nuclei; PY, Pyramid; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; VEN IV, Fourth Ventricle; VER, Vermis Cerebelli. [Accession No. 157. Section 310. Actual Size 30 × 32 mm.]

of the more highly differentiated species the convolution in the nucleus is pronounced. The chimpanzee stands intermediate between the two extremes of dentate differentiation. It presents the undulating and convoluted appearance in the outer wall of its structure. It is definitely sacculated in form; and it has a well-defined fundus. But the degree of the convolution is so marked as to encroach upon the fundus in such a way as to reduce materially its capacity for myelinized fibers.

What the configuration of the dentate nucleus of the chimpanzee may actually signify, and how it should be interpreted with reference to the functional capacity of this structure, are problems requiring further investigation. It is, however, worth noting that such a difference does exist in the chimpanzee and is sufficient to distinguish it from both the lower primates and the higher forms. It is possible that too much emphasis is laid upon this distinction and that this high degree of convolution in the saccular wall of the dentate nucleus really implies a far greater degree of specialization than in other species. On the other hand, the conditions as compared with those in man lead to the conclusion that specialization in chimpanzee, although along the lines of greater complexity, is not following the direction prescribed by the human mode of development which gives rise to a dentate nucleus in many characteristics quite different from that of the chimpanzee and much more in harmony with the gorilla. If any inference is justified with reference to the functional capacity of the cerebellum, it might properly be that the chimpanzee is endowed with coordinative control which is at least equal to that of the highest primate. The studies of behavior, already quoted in connection with the animal, emphasize the remarkable feats of strength and dexterity of the fore- and hindlimbs. They demonstrate a capacity for acquiring performances of a skilled nature, some of which surpass in their complexity those attainable by man. All of these facts signify that the chimpanzee possesses a range and variety of skilled performances which may easily rival those of the highest primates. That it does not apply these coordinative capacities in the execution of the many delicate and precise acts which characterize man concerns another department of its neural organization. That it is potentially equipped with and often does develop a surprising degree of such muscular regulation is a fact concerning which there can be no possible doubt.

The central gray matter forming the floor of the fourth ventricle contains the triangular nucleus of Schwalbe, lateral to which is Deiters' nucleus. Many fibers of the vestibular division of the eighth nerve enter the latter nucleus. Ventral to Deiters' nucleus is the substantia gelatinosa trigemini, in contact by its outer margin with the compact bundle forming the descending trigeminal tract. Contiguous with the outer margin of this tract and with Deiters' nucleus is a dense mass of myelinated fibers forming the restiform body, while upon the outer edge of this structure appears the tuberculum acusticum (Tub), into which many fibers of the acoustic division of the eighth nerve are entering. Upon the ventral surface of the section some of the features constituting the pons Varolii have become apparent. These consist of transverse fibers of the stratum superficiale surrounding a small scattered mass of nuclear substance, the pontile nuclei (PN), together with the tendency of the pyramidal tract to become disseminated by the interposition of nuclear substance and transverse pontile fibers. The boundary between the basis and the tegmentum is indicated, as at higher levels, by the tendency of the mesial fillet (Mf) to dispose itself transversely and thus serve as the line of demarcation between these two portions of the stem. Passing through the basis pontis, penetrating both the pontile nuclei and the pyramid, are some of the emerging fibers of the abducens nerve (N6). The cephalic tip of the inferior olivary nucleus occupies a position near the center of the reticular formation (Ref). The olivary nucleus is in relation to the dense bundle of fibers along its ventrolateral aspect constituting the central tegmental tract (Ctt) which serves as a connection between the olive and centers in the midbrain.

The reticular formation (Ref) is extensive but presents no marked specialization at this level. It is penetrated by many internal arcuate fibers. Some of these arcuate fibers occupying a more dorsal position in the reticular formation take their origin in the Deitersal nucleus and undergo decussation to form the crossed Deiterso-spinal tract. Other decussating fibers in a more ventral position pass inward to form the caudal portion of the corpus trapezoideum. This level is significant as showing the general tendency observed in the afferent course of all sensory pathways to undergo decussation. Usually the crossing of such pathways from one side to the other takes place in close relation to their nuclear origins. Such is the case with the pathway serving for afferent impulses from the upper extremity and trunk and the lower extremity and tail. For the impulses received from the proprioceptive structure of the internal ear, namely, the utricle, saccule and semicircular canals, a similar decussation takes place immediately after relay in the primary receiving stations of Deiters' and Schwalbe's nuclei.

LEVEL THROUGH THE PONS SHOWING THE EMERGENT FIBERS OF THE SIXTH NERVE, NERVUS ABDUCENS (FIGS. 263, 264)

At this level the contour of the section has undergone a marked change, due to the presence of the massive structures constituting the pons Varolii. The pons presents its characteristic three layers which consist of the stratum superficiale, the stratum complexum containing transverse pontile fibers, the pontile nuclei and the disseminated bundles of the pyramidal tract, and the stratum profundum consisting largely of transverse pontile fibers. Passing through the several strata of the pons are scattered fibers making their way forward to a point of emergence at the junction of the pons Varolii and the oblongata. These are the emergent fibers of the abducens nerve which supply the external rectus muscles of the eye (N6). The massive size of the pons, particularly the large volume of the pontile nuclei

(PN), signifies an animal in which there is a voluminous connection between the cerebral cortex and the lateral lobes of the cerebellum. Such a connection, as already mentioned in previous discussions, is indicative

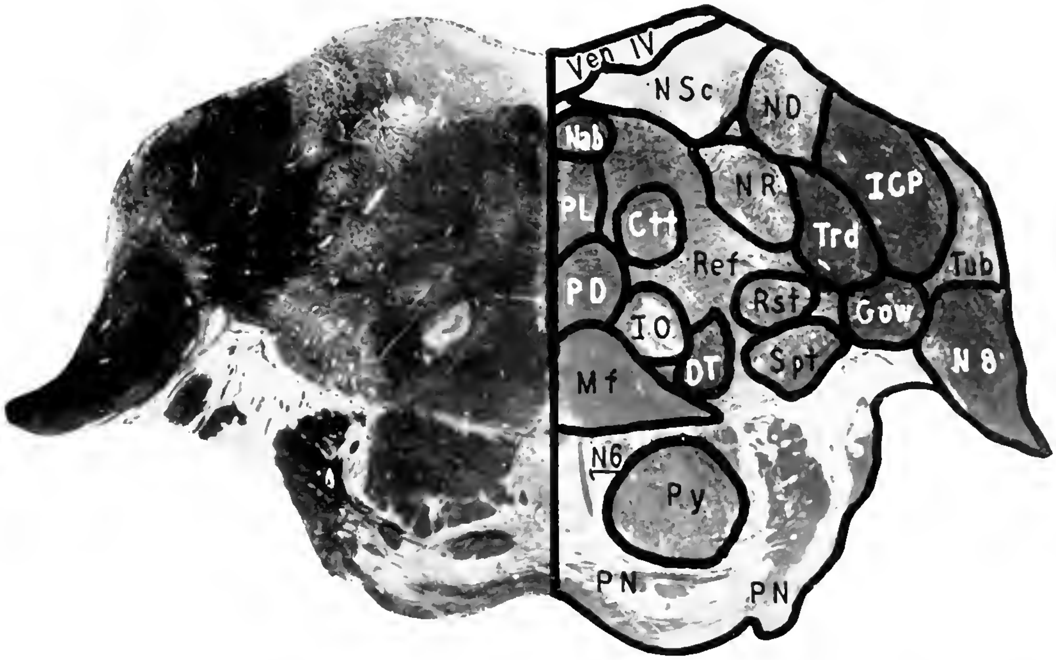


FIG. 263. CHIMPANZEE. LEVEL OF THE CAUDAL EXTREMITY OF THE PONS SHOWING THE EMERGENT FIBERS OF THE SIXTH NERVE.

CTT, Central Tegmental Tract; DT, Deiterso-spinal Tract; GOW, Ventral Spinocerebellar Tract; ICP, Inferior Cerebellar Peduncle; IO, Inferior Olive; MF, Mesial Fillet; NAB, Abducens Nucleus; ND, Deiters' Nucleus; NR, Nucleus of Rolando; NSC, Nucleus of Schwalbe; N6, Abducens Nerve; N8, Auditory Nerve; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PN, Pontile Nuclei; PY, Pyramid; RET, Reticular Formation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; TRD, Descending Trigeminal Tract; TUB, Tuberculum Acusticum; VEN IV, Fourth Ventricle. [Accession No. 157. Section 265. Actual Size 24 × 14 mm.]

of an animal in which skilled performances are developed to an unusually high degree. The pontile nuclei in themselves are significant of a rich palliocerebellar communication, but they also denote the possession of an intelligence relatively advanced in its development. The degree of this development has been carefully tested by various psychological and psychometric experiments. The general conclusion of various observers is that the standing of the chimpanzee among the primates gives this animal a place undoubtedly far below that of man, but yet sufficiently high to consider it capable of intelligent behavior.

FIG. 264. CHIMPANZEE. LEVEL THROUGH THE PONS SHOWING THE EMERGENT FIBERS OF SIXTH NERVE.

CTT, Central Tegmental Tract; MCP, Middle Cerebellar Peduncle; ML, Mesial Fillet; NBE, Nucleus of Bechterew; NAB, Abducens Nucleus; NDT, Cerebellar Nuclei, Mesial Group; NFG, Nucleus Fastigii; NR, Nucleus of Rolando; N5, Trigeminal Nerve; N6, Abducens Nerve; N7, Facial Nerve; PN, Pontile Nuclei; PY, Pyramid; RST, Rubrospinal Tract; SCP, Superior Cerebellar Peduncle; VEN IV, Fourth Ventricle. [Accession No. 157. Section 380. Actual Size 36 × 28 mm.]

In the central gray matter which here forms the floor of the fourth ventricle is a collection of nerve cells forming the nucleus abducentis (N a b). Into the ventricle projects the nodular portion of the inferior vermis, while the ventricular walls are marked by the dentate nucleus and its surrounding capsule of nerve fibers. Ventral to the tegmentum, and separated from it by the transversely disposed fibers constituting the mesial fillet (M f), is the basis pontis. All of the transverse fibers of the pons become collected to form a massive bundle proceeding laterally and dorsally to enter the cerebellum as the middle cerebellar peduncle (M c p).

LEVEL THROUGH THE MIDDLE OF THE PONS VAROLII (FIG. 265)

Here the contour of the section has undergone considerable modification, due to the fact that the ventricle has decreased in size as the caudal orifice of the Sylvian aqueduct is approached. It is bounded dorsally by the vermis of the cerebellum (V e r) and laterally by the two superior cerebellar peduncles (S c p). The central gray matter now forms the floor of the ventricle and immediately beneath this is a dense bundle of myelinized fibers which extends transversely and forms the genu facialis (N 7), the third portion of the emergent course of the facial nerve. The tegmentum is bounded ventrally by the bundles forming the mesial fillet (M f) and thus separated from the basis pontis, which comprises the characteristic pontile strata already described in this species. The transverse fibers of the pons are collected laterally to form the middle cerebellar peduncle (M c p) through which the fibers of the trigeminal nerve (N 5) make their way. The larger division of this nerve is situated dorsolaterally and constitutes the dorsal root fibers arising in the Gasserian ganglion. They represent dermatomic sensory areas of the head and face, supplied by the fifth cranial nerve. These fibers end in an irregular mass of gray matter forming the cephalic extremity of the substantia gelatinosa which, because of its convoluted appearance, is

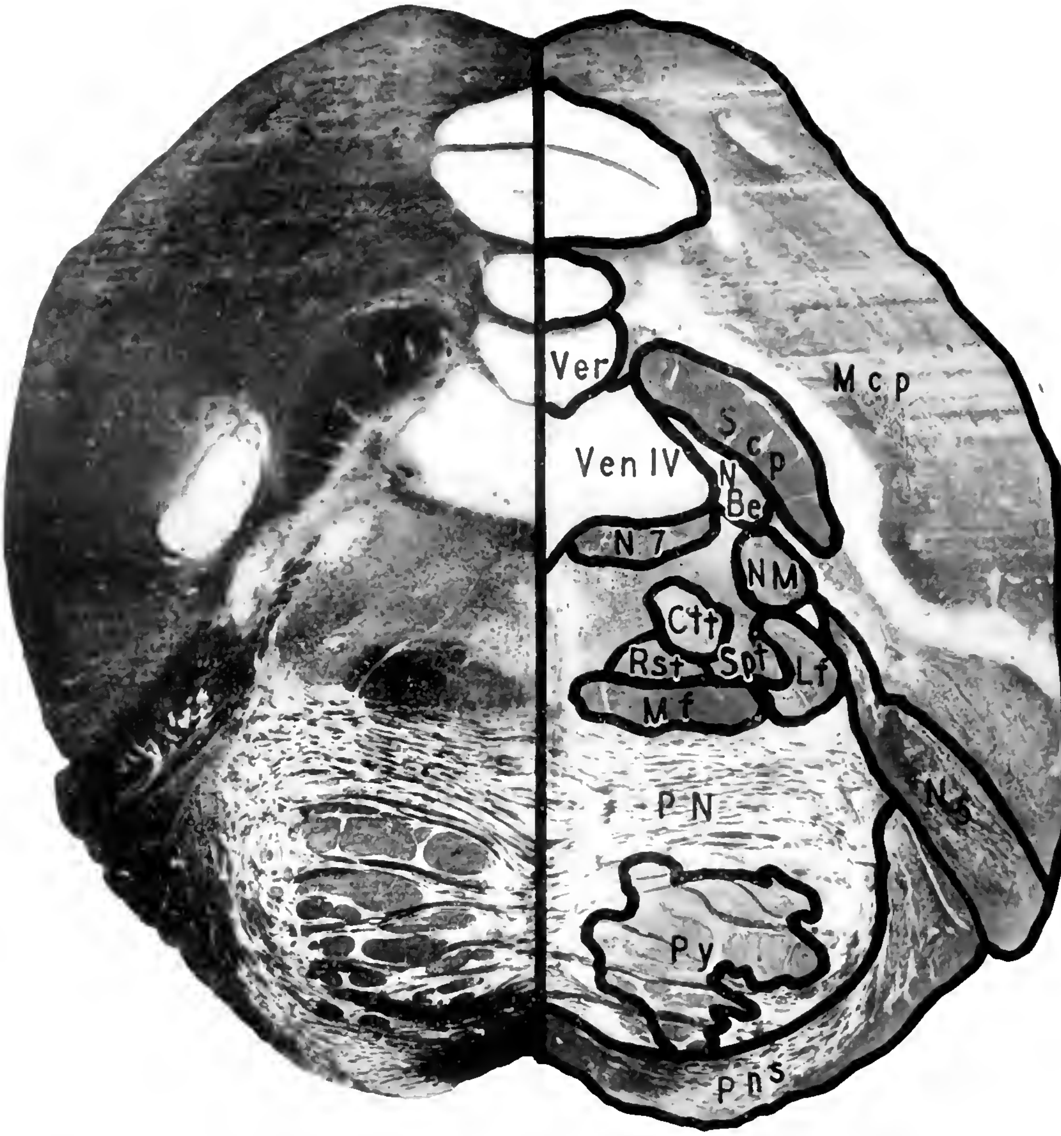


FIG. 265. CHIMPANZEE. LEVEL THROUGH THE MIDDLE OF THE PONS VAROLII.

CTT, Central Tegmental Tract; LL, Lateral Fillet; MCP, Middle Cerebellar Peduncle; ML, Mesial Fillet; NM, Nucleus Masticatorius; NBE, Nucleus of Bechterew; N5, Trigeminal Nerve; N7, Facial Nerve; PN, Pontile Nuclei; PNS, Pons; PY, Pyramid; RST, Rubrospinal Tract; SCP, Superior Cerebellar Peduncle; SPT, Spinothalamic Tract; VEN IV, Fourth Ventricle; VER, Vermis. [Accession No. 157. Section 305. Actual Size 28 × 27 mm.]

termed the convolutiones quinti. Mesial to the sensory root of the fifth nerve are the fibers of the motor division of the trigeminal nerve which supply the muscles of mastication. The origin of these fibers is plainly seen in the nucleus

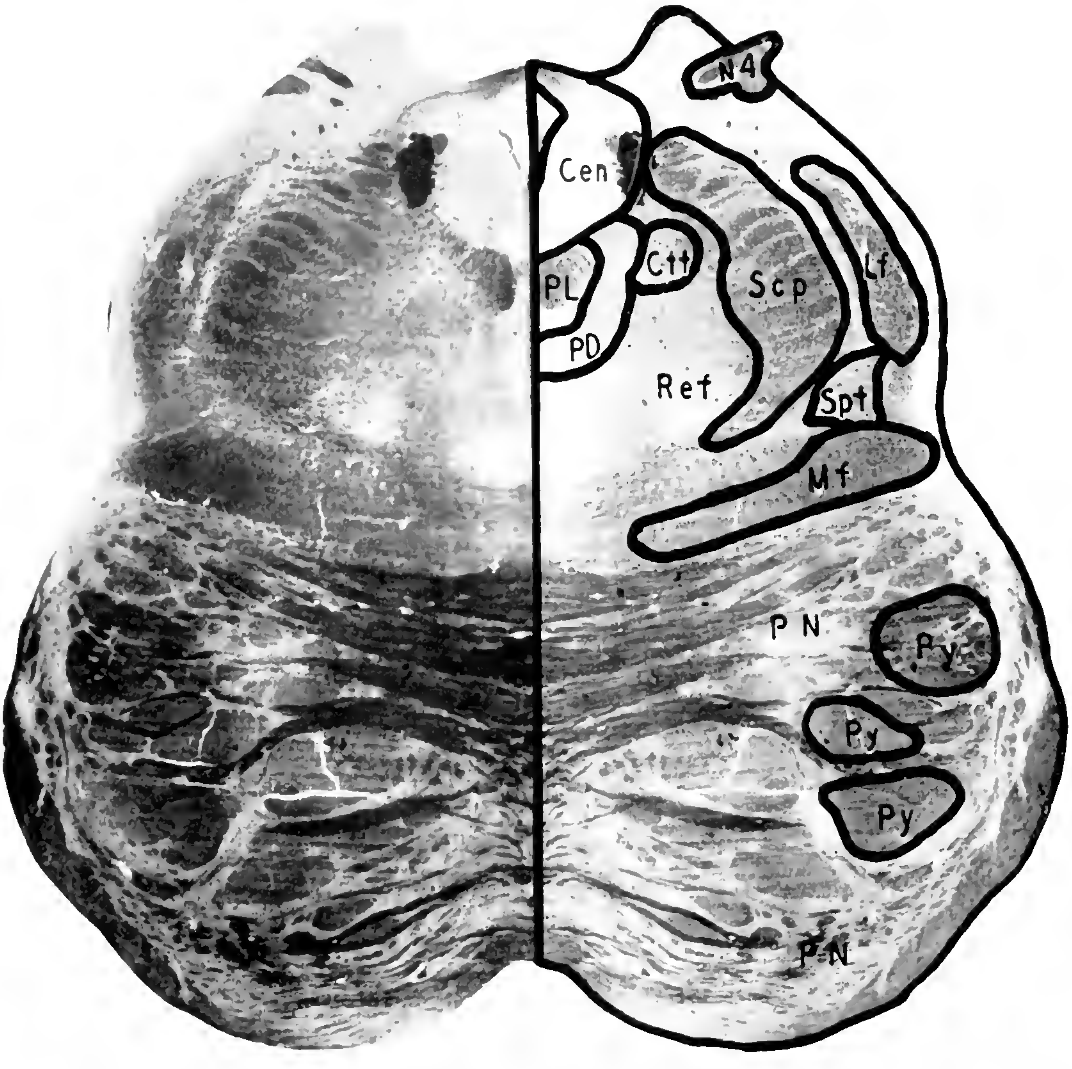


FIG. 266. CHIMPANZEE. LEVEL OF THE EMERGENCE OF THE FOURTH NERVE.

CEN, Central Gray Matter; CTT, Central Tegmental Tract; LF, Lateral Fillet; MF, Mesial Fillet; N4, Trochlear Nerve; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PN, Pontile Nuclei; PY, Pyramid, RET, Reticular Formation; SCP, Superior Cerebellar Peduncle; SPT, Spinothalamic Tract. [Accession No. 157 Section 505. Actual Size 21 × 10 mm.]

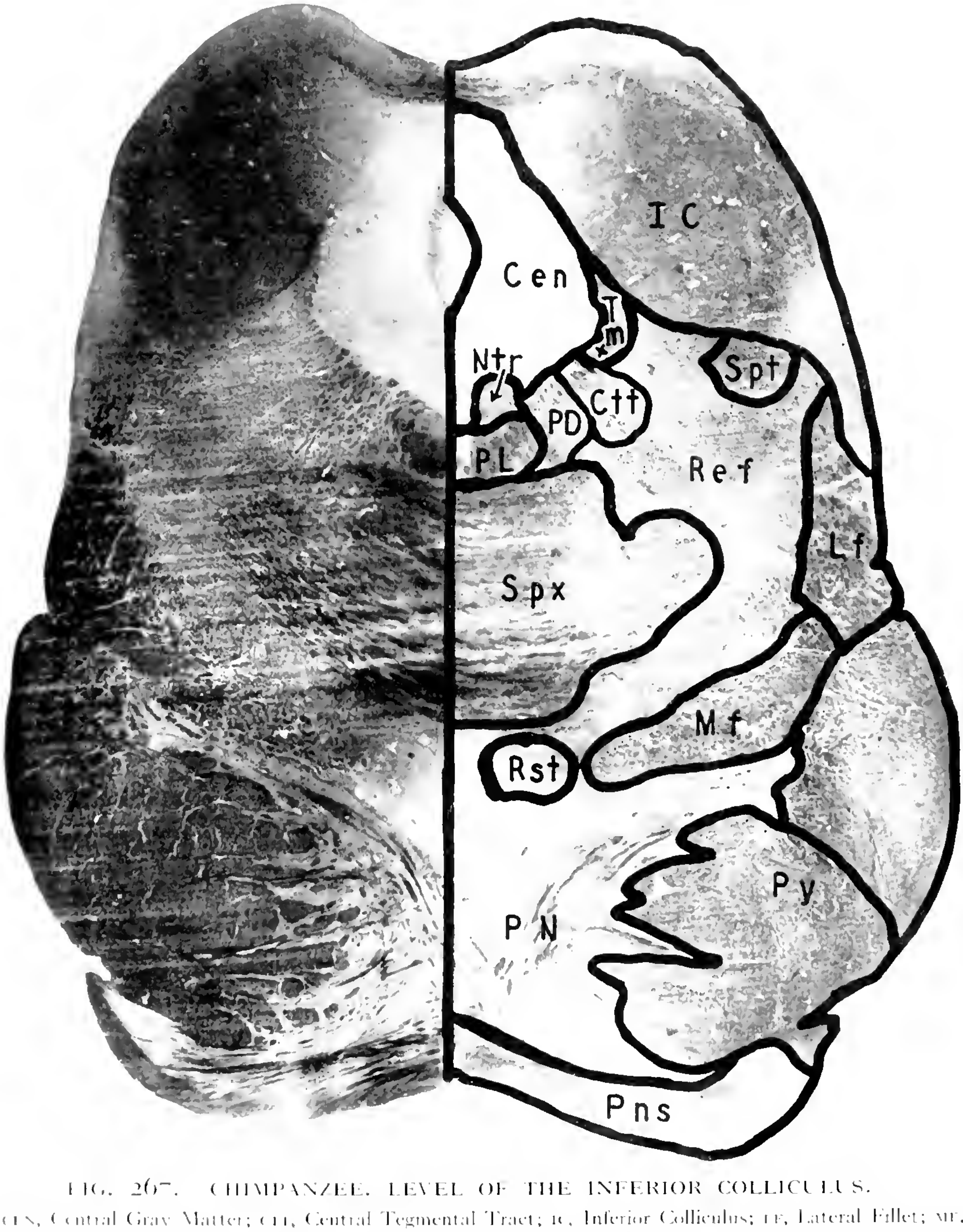


FIG. 267. CHIMPANZEE. LEVEL OF THE INFERIOR COLLICULUS.

CEN, Central Gray Matter; CTT, Central Tegmental Tract; IC, Inferior Colliculus; LF, Lateral Fillet; MF, Mesial Fillet; NTR, Nucleus Trochlearis; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PN, Pontile Nuclei; PNS, Pons; PY, Pyramid; RLF, Reticular Formation; RST, Rubrospinal Tract; SPT, Spino-thalamic Tract; SPX, Crossing of the Superior Cerebellar Peduncle; TMT, Ascending Mesencephalic Tract of the Fifth Nerve. [Accession No. 157. Section 170. Actual Size 19 × 19 mm.]

situated ventromesial to the convolutiones quinti, constituting the nucleus masticatorius (NM). The diffuse reticular formation occupies nearly the entire field of the tegmentum and is not differentiated to form any specialized nuclear aggregation. This level is significant as offering some basis for estimating the degree to which the fifth cranial nerve contributes to the influx of sensory impulses from the body, particularly as this innervation bears upon the direction of the animal's motor control.

LEVEL OF THE INFERIOR COLLICULUS (FIG. 267)

At this level, changes incident to the appearance of the two caudal elevations in the quadrigeminal plate have altered the contour of the section. In this region the ventricular chamber has been reduced in its dimensions to those characteristic of the Sylvian aqueduct which is now entirely surrounded by the central gray matter (Cen). In the ventromesial portion of this substance is a specialized region forming the nucleus trochlearis (Ntr). A dense bundle of fibers passing from this nucleus constitutes the first portion of the emergent course of this motor nerve. At the lateral periphery of the central gray matter is a band-like collection of fibers, somewhat separated into small fasciculi, forming the ascending mesencephalic tract of the fifth nerve (Tmt).

The most outstanding features, however, are the two elevations above the central gray constituting the inferior colliculi (IC) to which some fibers of the lateral fillet are making their way. This colliculus is a way-station in the pathway of auditory impulses destined for the temporal lobe of the cerebral cortex. It still shows some of its primitive histological details, especially indicated by the rudimentary stratification of cell and fiber layers. Comparatively speaking, however, the inferior colliculus is less prominent in the chimpanzee than it is in the intermediate and lower primates, thus indicating that its original and predominant function with reference to the sense of hearing has decreased considerably in importance. Such recession is due to the fact that the auditory activities have been taken over by a higher portion of the nervous system, namely, the temporal area of the cerebral hemisphere. Much emphasis has been laid upon the significance of this portion of the brain stem in its bearing upon the evolutional process which has operated in the interest of giving to the sense of hearing a more expansible and more cooperative cerebral region for the elaboration of the auditory sense. The roof of the midbrain was so placed as to be definitely embarrassed by its topography, since any expansion in the endbrain must necessarily be attended by corresponding development of the cerebellum. The mesencephalic roofplate, from which the inferior colliculi arise, under such conditions would be caught between two slowly expanding structures,namely, the endbrain in front and the cerebellum behind. In any case, a delegation of midbrain function to the hemispheres has taken place and the dimensions of the inferior colliculus have correspondingly decreased.

Considered in terms of functional significance, it appears that auditory sense has become less important as represented in the midbrain of the chimpanzee than it is in the lower primates. The inferior colliculi are connected across the midline by means of medullated commissural fibers. The tegmentum in this region of the midbrain is separated from the basis by the interposition of the mesial fillet (Mf) and the central portion of the field is occupied by the decussation of the superior cerebellar peduncle (Spx) preparatory to its entrance into the red nucleus at a somewhat higher level. In the basis of the section are many of the characteristic pontile features, while on the ventral surface a deepening of the median sulcus is about to determine the separation of the two halves of this region of the stem to form the cerebral peduncles. This section is important because of its bearing upon the function of hearing, particularly as that function appears to be undergoing delegation to higher and more efficient areas of synthesis in the cerebral cortex.

LEVEL OF THE SUPERIOR COLLICULUS (FIG. 268)

At this level two modifications have occurred to distinguish the section; first, the separation of the basal region of the axis to form the two cerebral peduncles (CP) with the production of an interval between them the optico-peduncular space; second, in a dorsal position, the appearance of the two cephalic elevations of the quadrigeminal plate constituting the superior colliculi (SC). These structures are associated with the visual pathway and are the vestigial remnants of formerly prominent structures forming the optic lobes. Their functional significance, as in all the primates, arises from the fact of their decline in structural prominence and the attendant diminution in functional importance with reference to vision. The same process involved in the differentiation of the inferior colliculus has been in progress in this portion of the midbrain. A progressive delegation of visual function to new and more expansible areas of the cerebral cortex has proceeded, until nearly all of the visual activities have been advanced to the occipital lobes. The superior colliculus, however, still bears some evidence of its former dominance in vision and retains a few of the original fourteen layers of this portion of the tectal cortex. At best the differentiation of these layers is indefinite and indicative of an area in process of decline.

The central gray matter (Cen) entirely surrounds the Sylvian aqueduct and in its central region is elongated for the specialization of the large oculomotor nucleus (Noc) which gives rise to the fibers of the oculomotor nerve (N3). Fibers arising in this nucleus make their way forward to emerge from the brain stem in the optico-peduncular space from the oculomotor sulcus.

More important than the emergent fibers of the oculomotor nerve are the commissural and decussating axons which connect the nuclei of the two sides. The extensiveness of this internuclear connection in chimpanzee is

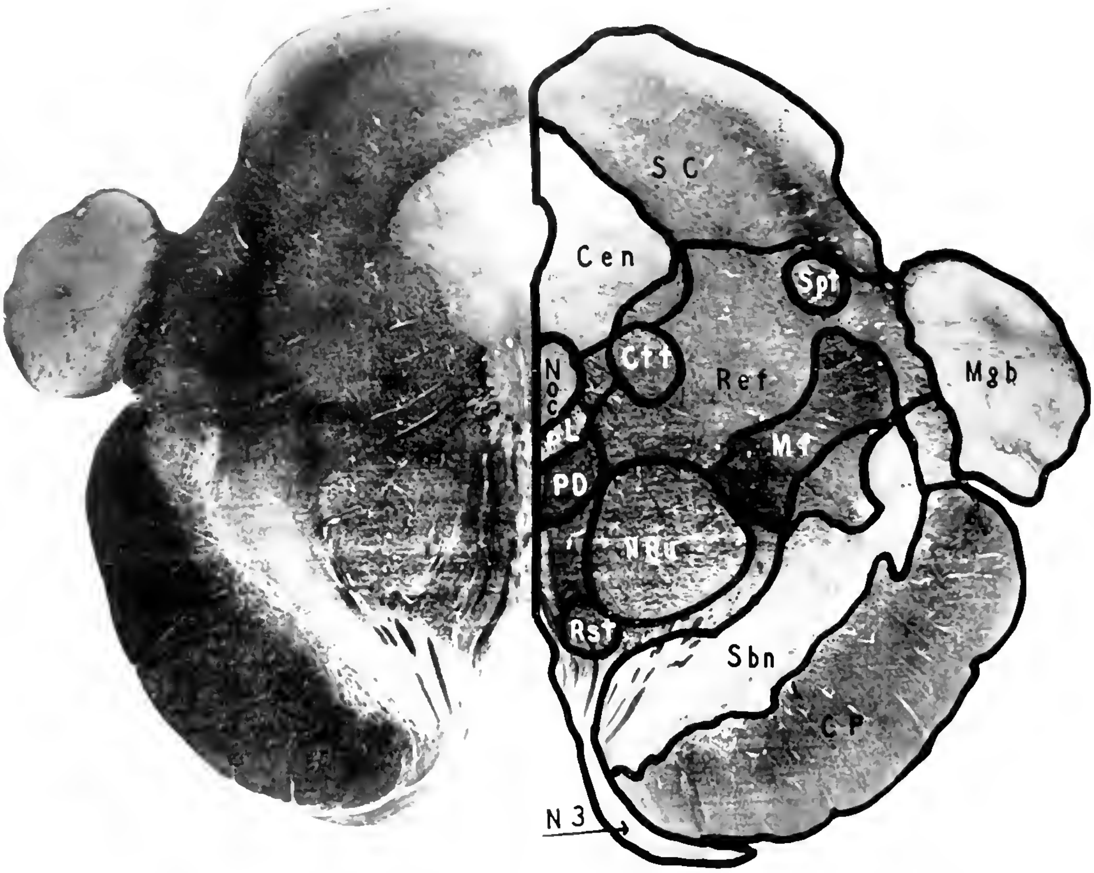


FIG. 268. CHIMPANZEE. LEVEL OF THE SUPERIOR COLLICULUS.
CEN, Central Gray Matter; CP, Cerebral Peduncle; CTT, Central Tegmental Tract; MF, Mesial Fillet; MGB, Mesial Geniculate Body; NOC, Oculomotor Nucleus; NRU, Nucleus Ruber; N3, Oculomotor Nerve; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; REF, Reticular Formation; RST, Rubrospinal Tract; SBN, Substantia Nigra; SC, Superior Colliculus; SPT, Spinothalamic Tract. [Accession No. 157. Section 530. Actual Size 26 × 13 mm.]

notable, since this intercommunication is related to binocular and stereoscopic vision. This animal possesses a fairly high degree of such vision. The tests made by most careful psychological investigations, particularly in the hands of Professor Köhler, have definitely disclosed the fact that the chimpanzee is able to employ stereoscopic fusion effectively. In conjunction with the extensive oculomotor connection between the two nuclei, this fact goes a long way to substantiate the theory advanced concerning the function of this decussation.

On the boundary line between the basis and tegmentum is a massive aggregation of gray matter which extends from the lateral periphery where it appears to be in continuity with the mesial geniculate body (Mgb) transversely across the section to the margin of the optico-peduncular space. This is the substantia nigra (Sbn) the functional significance of which is not altogether clearly understood, but to which is attributed the function of control over automatic associated movements. Whatever its functional capacity may be, it is clear in the ascending series of the primates, that the nuclear structure becomes more definitely outlined but somewhat smaller in size. The reticular formation (Ref) contains at this level a highly specialized nuclear structure situated near the midline. This is the nucleus ruber (NRu), the way-station in the pathway out of the cerebellum which serves in the capacity of conveying impulses to the muscles necessary to coordinative control. Its large size and clear definition of outline in chimpanzee indicate a structure engaged in functional activities of the greatest importance. In contrast with the similar nucleus in the lower primates, as well as in the intermediate group, the red nucleus has increased both in size and in clearness of definition. This, so far as the chimpanzee is concerned, would indicate definite augmentation in the function of muscular coordination. Such interpretation is in keeping with the fact that the dentate nucleus has similarly increased in this species.

The basal portion of the axis consists of a dense medullary structure constituting the cerebral peduncle (CP) and containing heavily myelinized fibers of the pallio-ponto-cerebellar and the pyramidal systems. From its size may be estimated the degree to which the animal has developed not only its volitional control, but that regulation of motion dependent upon the harmonious cooperation between the several lobes of the cerebral hemi-

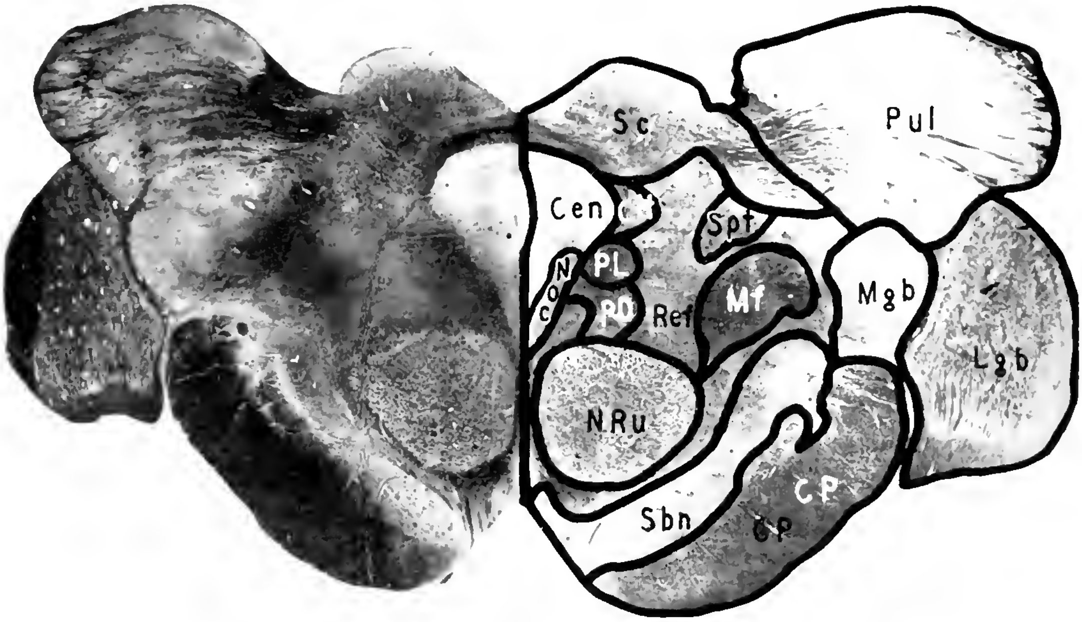


FIG. 269. CHIMPANZEE. LEVEL OF THE LATERAL GENICULATE BODY.
CEN, Central Gray Matter; CTT, Central Tegmental Tract; CP, Cerebral Peduncle; LGB, Lateral Geniculate Body; MGB, Mesial Geniculate Body; MF, Mesial Fillet; NOC, Oculomotor Nucleus; NRU, Nucleus Ruber; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PUL, Pulvinar; RTF, Reticular Formation; SC, Superior Colliculus; SBN, Substantia Nigra; SPT, Spinothalamic Tract. [Accession No. 157. Section 675. Actual Size 38 × 15 mm.]

spheres and the lateral lobes of the cerebellum. Its dimensions in chimpanzee thus indicate a high degree of organization in these particulars.

LEVEL OF THE LATERAL GENICULATE BODY (FIG. 269)

This section is introduced largely with the purpose of showing the conspicuous dimensions and appearance of the nucleus ruber (NRu). Some fibers in the oculomotor decussation are still seen in connection with the oculomotor nucleus (Noc). Laterally, both mesial and lateral geniculate bodies are shown (Mgb, Lgb), the latter receiving fibers making their way inward through the optic tract on their way to the visual area of the cerebral cortex. The geniculate bodies, both mesial and lateral, apparently have developed in the interest of that delegation of auditory and visual function to the cerebral cortex which is characteristic of the mammalian brain and have become progressively more conspicuous in the primate series. The superior extremity of the colliculi is also seen and lateral to it another relay station connected with visual function, the pulvinar of the optic thalamus (Pul). The section is particularly important because of the clear definition of the red nucleus (N Ru), thus offering another criterion by which to judge the degree of coordinative specialization in the chimpanzee.

LEVEL OF THE OPTIC CHIASM (FIG. 270)

At this level the contour has been changed by the appearance of the vertical third ventricle and the extensive lateral masses of the thalami bounding it upon either side. The continuity of the third ventricle is interrupted by the appearance at this level of the large commissura mollis. The optic thalami here are separated laterally from the globus pallidus of the corpus striatum (Glp) by the interposition of a dense mass of myelinized fibers constituting the internal capsule (Cin). This latter structure is the continuation cephalad of the cerebral peduncle and serves to establish the final connection with the cerebral cortex. In the internal capsule at this level are fibers of the pallio-ponto-cerebellar system, and also of the pyramidal system. The most ventral structure of the section is the optic chiasm (Opx), along whose dorsal aspect passes a set of less densely myelinized fibers constituting the supra-optic decussation of Meynert. The optic chiasm serves as the point of partial crossing in the visual pathway, receiving at its cephalic angles the two optic nerves and being continuous at its caudal border with the optic tracts. These latter together with the cerebral peduncles form the lateral boundary of the optico-peduncular space. The optic thalami provide the important relay stations in the pathway of all types of sensibility with the exception of the olfactory

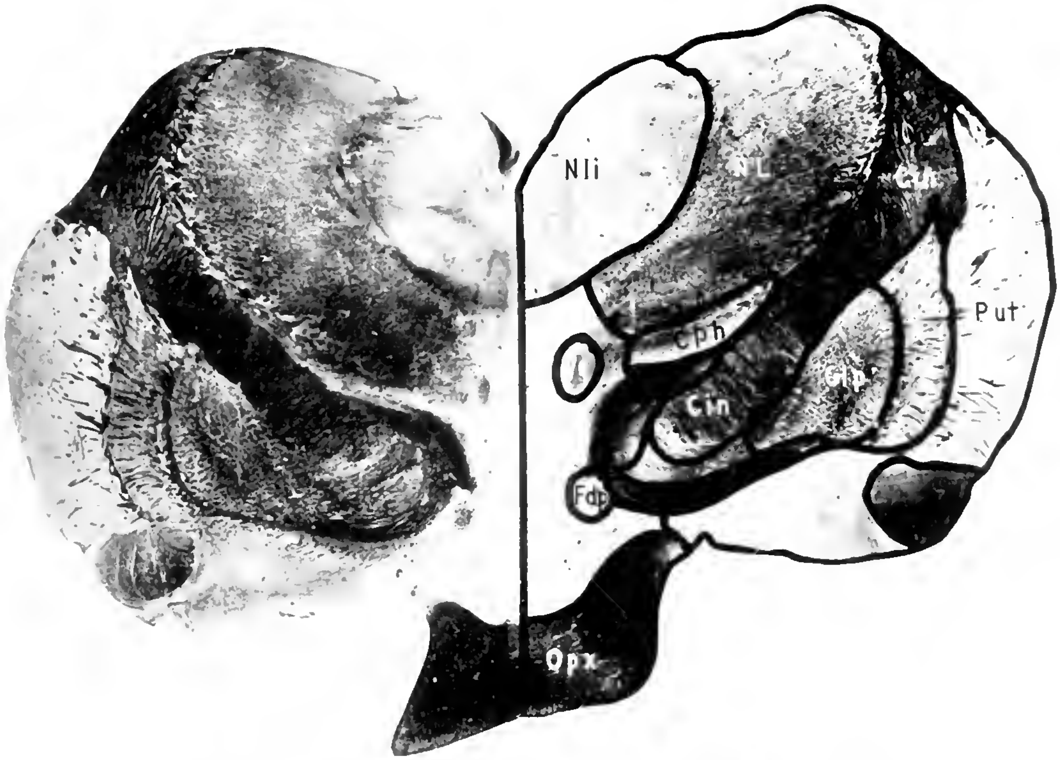


FIG. 270. CHIMPANZEE. LEVEL OF THE OPTIC CHIASM.

CIN, Internal Capsule; FDP, Descending Pillars of Fornix; FPH, Corpus Hypothalamicum; GLP, Globus Pallidus; NL, Lateral Nucleus of Thalamus; NLI, Internal Lateral Nucleus of Thalamus; OPX, Optic Chiasm; PUT, Putamen; VQ, Fasciculus of Vicq D'Azyr. [Accession No. 157. Section 813. Actual Size 45 × 25 mm.]

sense. The specializations within this portion of the brain stem are too extensive to permit of discussion at this time and properly belong to a treatise in which exclusive attention may be devoted to their structure and evolutional significance. The globus pallidus (Glp), a portion of the corpus striatum, likewise is a structure presenting a high degree of specialization. Being a part of the endbrain it should properly be considered with other constituents of this division of the encephalon rather than as related to the brain stem.

LEVEL OF THE ANTERIOR COMMISSURE (FIG. 271)

At this level the section indicates the extreme cephalic limit of the brain stem. In it are shown the cephalic portion of the third ventricle (Ven III)

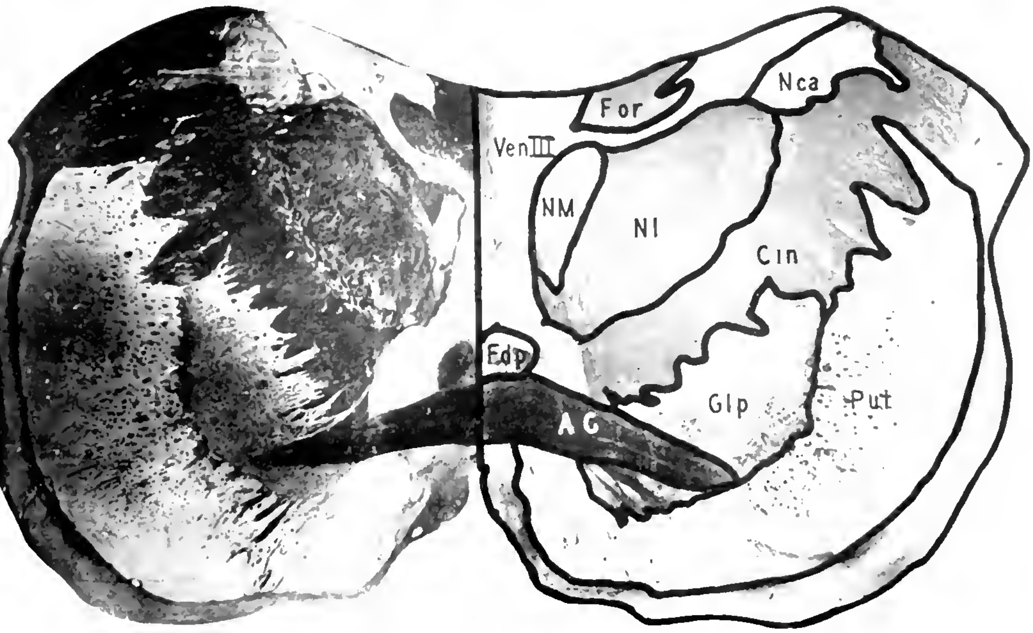


FIG. 271. CHIMPANZEE. LEVEL OF THE ANTERIOR COMMISSURE.
AC, Anterior Commissure; CIN, Internal Capsule; FDP, Descending Pillar of Fornix; FOR, Fornix; GLP, Globus Pallidus; NCA, Caudate Nucleus; NI, Lateral Nucleus of Thalamus; PUT, Putamen; NM, Nucleus Masticatorius Trigemini; VEN III, Third Ventricle. [Accession No. 157. Section 909. Actual Size 45 × 17 mm.]

approaching the lamina terminalis and bounded upon either side by the cephalic portion of the optic thalami. Overlying the roof of the third ventricle is the compact mass of fibers forming the corpus callosum, dependent from which are portions of the anterior pillars of the fornix (For) Beneath the floor of the ventricle passes the anterior commissure (AC) connecting one hemisphere with the other, the most cephalic link of communication. Separating the cephalic extremity of the optic thalamus from the globus pallidus of the corpus striatum is a dense bundle of fibers constituting the anterior limb of the internal capsule (Cin). The more important structures in the section are indicated by appropriate letters in the caption.

Chapter XX

RECONSTRUCTION OF THE GRAY MATTER IN THE BRAIN STEM OF TROGLODYTES NIGER

IN the reconstruction of the high cervical level of the spinal cord, the ventral gray column has already been separated from the central gray matter by the decussation of the pyramidal tract. The central gray matter itself is quadrilateral in shape with a ventromedian prolongation. It is situated in its usual central position.

The ventral gray column is irregularly triangular in outline with its base directed ventromesially, its apex ventrolaterally. The dorsal horns are long, compressed laterally and situated almost in the transverse meridional line of the cross section. Their peripheral expansion forming the substantia gelatinosa trigemini is bulky, roughly oval and presents the tendency towards the rather flame-like configuration which has been found to be characteristic of this nuclear mass.

The sensory nucleus of Goll has already made its appearance, being elongated from before backward and lying as a more or less laterally compressed strand of gray matter within the fibers of the column of Goll. It is surrounded on all sides, except at the base, where it is confluent with the central gray matter, by the enveloping fibers of the column of Goll.

In general, the high level of the cervical spinal cord is identical in arrangement with cross sections of the human brain stem. It becomes apparent in the studies of these simian sections that the human pattern is being more closely approached, both in extent and in complexity of organization. Many of the levels of the chimpanzee and of gorilla are indistinguishable from similar sections of the human neuraxis.

The Dorsal Medullary Nuclei

One of the dorsal sensory nuclei has already made its appearance. The nucleus of Goll is present and occupies almost the entire ventrodorsal extent of the column of Goll. It is narrow, compressed from side to side and connected at its base with the central gray matter. On all sides, except at its point of junction with the central gray matter, it is enveloped by fibers of the column of Goll. The sensory nucleus of Burdach first appears at a level somewhat higher than the caudal extremity of the nucleus of Goll. It is distinguishable as a thickening in the dorsal surface of the central gray matter or the junction of the dorsal horn with the central gray matter. This sessile condensation of nuclear material gradually becomes more prominent.

A lateral divergence is characteristic of all of the dorsal gray structures, being produced by the opening of the fourth ventricle which tends to force all of the dorsal structures further from the median line. The dorsal extremity of the nucleus of Goll becomes expanded laterally and overhangs the more ventral structure at a level below the opening of the expanding fourth ventricle. The nuclear material becomes much more extensive near the dorsal periphery of the axis and presents a marked tendency to accumulate laterally. This arrangement is characteristic also of the nucleus of Burdach, the dorsal extremity of which becomes heavier and shows the same tendency towards lateral extension. In some places it is carried so far as to overhang the substantia gelatinosa trigemini.

In the caudal region of the ventricular opening the lateral walls of the fourth ventricle on each side are formed by the nucleus of Goll. Higher up the nucleus of Goll is gradually separated from the lateral borders of the fourth ventricle by the interposition of the vestibular complex between it and the ventricular wall.

Shortly after the appearance of this nuclear mass the nucleus of Goll begins to diminish. The diminution of this nuclear mass continues rapidly until the entire column with its nucleus disappears.

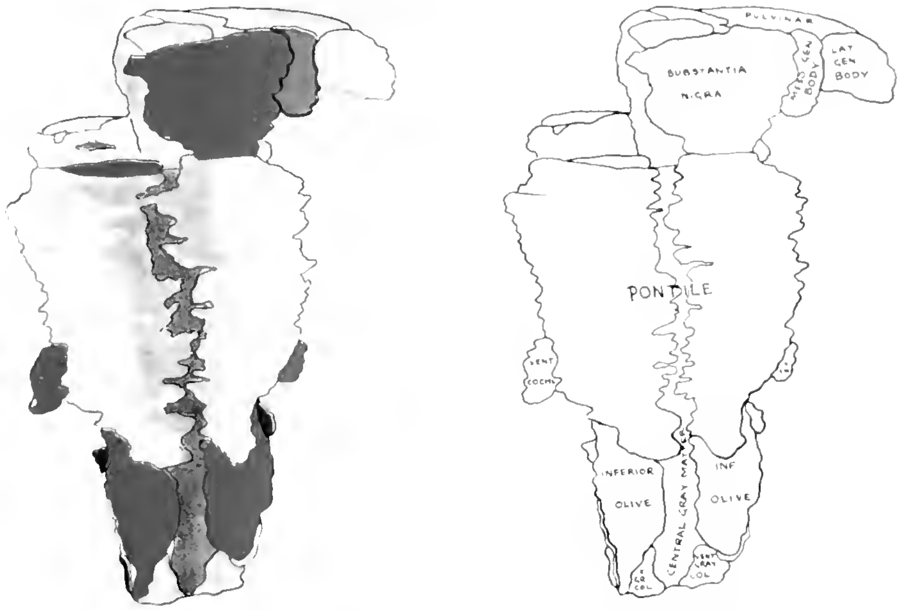


FIG. 272. VENTRAL SURFACE OF GRAY MATTER OF BRAIN STEM, TROGLODYTES NIGER.

KEY TO DIAGRAM. INF. OLIVE, Inferior Olive; LAT. GEN. BODY, Lateral Geniculate Body; MESO-GEN. BODY, Mesial Geniculate Body; PONTILE, Pontile Nuclei; V. CH. and VENT. COCH., Ventral Cochlear Nucleus; V. GR. COL. and VENT. GRAY COL., Ventral Gray Column.

The nucleus of Burdach reaches its maximum at the level of disappearance of the nucleus of Goll. It then gradually diminishes and comes to an end below the mid-ventricular level.

The substantia gelatinosa trigemini described in connection with the high cervical level of the spinal cord gradually passes more into the latero-meridianal position, which is characteristic of this structure. Having reached this position it continues upward almost unchanged to the upper level of the pontile portion of the stem where it finally becomes expanded as the convolutiones quinti.

At a point somewhat below the mid-ventricular portion of the stem the substantia gelatinosa shows the attenuation which is characteristic of this nucleus and which here had been termed the "waist" of the nucleus. Passing cephalad, however, it rapidly expands again and appears as a prominent feature in the cross section of the pontile region. Its mesial surface is in close contact with the reticular formation of the myelencephalon and metencephalon, which is hollowed out to receive this trigeminal nucleus. As the point of transition between the metencephalon and the mesencephalon is approached the nucleus gradually begins to disappear and it finally merges insensibly into the reticular formation of the upper metencephalon.

The Inferior Olivary Nucleus

This nuclear mass of gray matter has attained relatively large proportions in the oblongatal sections. It is both extensive in size and complicated in structure. Its fundus and the two branches which compose it are made up of a complex series of plications and reduplications which thus greatly increase the cell-bearing area of the nucleus. The fundus is deep and directed toward the ventrolateral angles of the oblongata. It reaches almost to the periphery and produces a well-marked prominence on the surface of the oblongata, the olivary eminence. It begins below at a point corresponding to the caudal end of the nucleus of Burdach and extends upward through the metencephalon to a level corresponding with the maximum development of the vestibular complex.

The ventral accessory olivary nucleus is present as a well-developed lamina of gray matter arising at almost the lowest level of the chief nucleus as a small collection of nuclear material in front of the ventral branch of the main nucleus. It continues upward closely applied to this ventral branch, to the cephalic extremity of the nucleus, where it gradually disappears by becoming confluent with the dorsal extension of the ventral branch.

The dorsal accessory nucleus presents a somewhat similar arrangement consisting of a thin lamina of gray matter applied to the surface of the dorsal branch of the main nucleus. It extends upward for about the same distance

FIG. 273. DORSAL SURFACE OF GRAY MATTER OF BRAIN STEM, TROGLODYTES NIGER.

KEY TO DIAGRAM. DORSAL COCHLEAR, Dorsal Cochlear Nucleus; INF. COLL., Inferior Colliculus; LAT. GENICULAT. BODY, Lateral Geniculate Body; MESO-GENICULATE BODY, Mesial Geniculate Body; NUCL. OF BURDACH, Nucleus of Burdach; NUC. OF DEITERS and NUCL. OF DEITERS, Nucleus of Deiters; NUCL. OF GOLL, Nucleus of Goll; RET. FORM., Reticular Formation; SUBST. GEL. ROLANDO, Substantia Gelatinosa of Rolando; VENT. COCH., Ventral Cochlear Nucleus.

as the main nucleus and cephalically comes to an end by becoming confluent with the dorsal branch of the nucleus. The dorsal surface of the main nucleus as well as the dorsal accessory nucleus are embedded in the ventral aspect of the reticular formation and are therefore hidden from view in the reconstruction. The ventromesial surface of the nucleus is in contact with the pyramid, the fillet and other tracts of the ventral field of the oblongata.

The Reticular Formation

The reticular formation appears at a level corresponding to the beginning of the pyramidal decussation as an accumulation of white and gray matter lateral to the remnants of the ventral gray column. It lies in the meshes between the decussating pyramidal fibers. As the pyramidal tracts gradually fuse in the median line, this formation assumes greater prominence. The ventral gray columns, as they ascend, are increasingly broken up by the bundles of the pyramidal tract and therefore acquire an arrangement characteristic of the reticular formation, within which latter they finally disappear. The reticular formation becomes more massive in the metencephalon in which segments are found those various condensations forming important neuraxial nuclear masses. In outline the reticular formation is more or less rectangular, presenting lateral, mesial, ventral and dorsal borders. The lateral border is covered only by white fibers and extends almost to the periphery of the cord, lying between the inferior olivary nucleus and the substantia gelatinosa trigemini. Its ventral aspect is extensive and receives the dorsal surface of the inferior olivary complex. Its mesial border is located near the raphe between the dorsal extremities of the inferior olivary nucleus and the ventral gray matter, while its dorsal extent is applied to the ventral surface of the central gray matter as this structure spreads out to form the floor of the fourth ventricle. This disposition is continued upward, the reticular formation forming the main mass of the tegmentum of the brain stem. It contains various fiber tracts and forms the matrix for the development of several nuclear collections. It provides the general support for the entire tegmental structure. The two mesial surfaces are placed opposite one another, each being separated from its fellow by the longitudinal bundles which make up the raphe.

With the development of the pontile nuclei the ventral surface of the reticular formation comes into relationship with these structures.

The ventral surface of the reticular formation enters into intimate relationship with the dorsal extremity of the lateral and mesial buttresses which form the main mass of the pontile nuclei. Between these two areas of con-

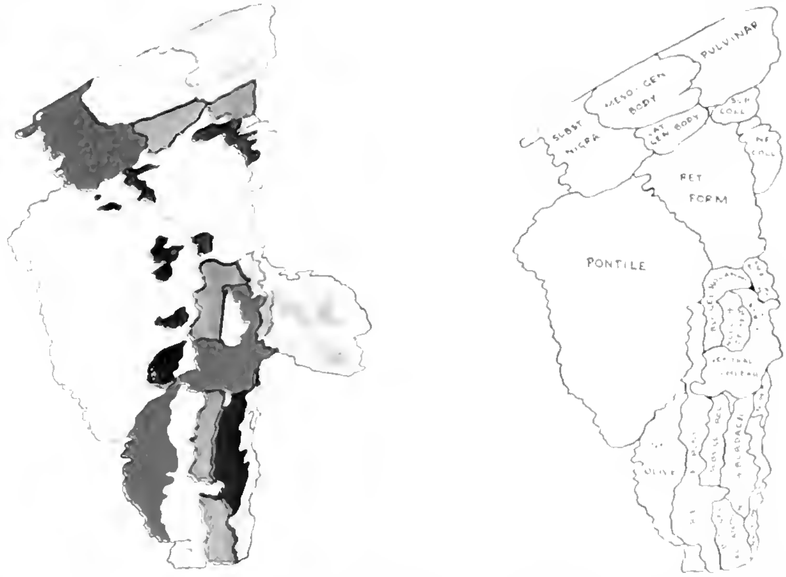


FIG. 274. LATERAL SURFACE OF GRAY MATTER OF BRAIN STEM, TROGLODYTES NIGER.

KEY TO DIAGRAM. DORSAL COCHL., Dorsal Cochlear Nucleus; INF. COLL., Inferior Colliculus; INF. OLIVE, Inferior Olive; LAT. GEN. BODY, Lateral Geniculate Body; MESO-GEN. BODY, Mesial Geniculate Body; NUCL. OF BURDACH, Nucleus of Burdach; N. OF D. and NUCL. OF DEITERS, Nucleus of Deiters; NUCL. OF GOLL, Nucleus of Goll; RET. FORM., Reticular Formation; SUBS. GEL. ROL. and SUBST. GEL. ROLANDO, Substantia Gelatinosa of Rolando; SUBST. NIGRA, Substantia Nigra; SUP. COLL., Superior Colliculus; VENTRAL COCHLEAR, Ventral Cochlear Nucleus.

tact the dorsal surface of the deep layer of the pontile nucleus does not fuse with the ventral surface of the reticular formation, since in this area the trapezoid body and the other peripheral condensation of fibers develop.

As the mesencephalon is approached the reticular formation replaces the substantia gelatinosa trigemini and the upper part of the vestibular complex as these structures diminish and finally disappear. In this region the formation extends backward until it comes into contact with the central gray matter. Its lateral portion is tunnelled from behind forward and from without inward by the superior cerebellar peduncle as this mass of fibers passes deeper into the tegmentum. At the point where the superior cerebellar peduncle leaves the superior medullary velum and approaches the tegmentum a thin extension of the reticular formation forms on its lateral aspect. This thin layer passes further dorsad until the superior cerebellar peduncle is completely surrounded by mesencephalic reticular formation. From this point the peduncle sinks deeply into the tegmentum of the pons, tunnelling the reticular formation of the upper part of the metencephalon and the lower levels of the mesencephalon until it reaches the midline where it decussates. A termination for most of its fibers is provided in the nucleus ruber.

Just above the termination of the substantia gelatinosa trigemini the lateral extension of the reticular formation is grooved by the passage of the lateral fillet. This prolongation of the reticular formation gradually envelops the lateral fillet as the latter sinks into the tegmentum to end in connection with the inferior colliculus.

The formatio reticularis comes into such close contact with the surface of the mesencephalon that its lateral conformation is almost identical with the surface of this segment of the neuraxis. It is separated from the lateral angle of the inferior colliculus by a space in which develops the group of fibers forming the inferior brachium.

Above this point the reticular formation seems to diminish in volume and becomes confluent with the indifferent gray matter of the epithalamic and hypencephalic formations. Laterally it merges with the reticular formation of the dienecephalon.

Between the superior and inferior colliculi the reticular formation gains the surface of the mesencephalon in the intercollicular furrow. Cephalically it forms the lateral and ventral support for the deep surface of the superior colliculus. It does not come into contact with the superficial layers of the colliculus due to the development of the superior brachium which passes from the lateral aspect of the superior colliculus to the lateral geniculate body.

In the upper levels of the mesencephalon the reticular formation is to a great extent replaced in its ventral portion by the nucleus ruber. Dorsal to the nucleus ruber, however, a portion of the formation remains and continues upward to merge with the reticular formation of the dienecephalon.

The Pontile Nuclei

The pontile nuclei present an exceedingly complicated appearance. They begin below as the arciform nuclei which first appear at about the mid-olivary level. The arciform nuclei form a relatively simple layer of gray matter surrounding the pyramid. This pyramidal investment creeps further laterad until the nuclear material extends completely around the pyramidal tract. The amount of nuclear material increases, presenting an extreme complexity in its development. It still maintains, however, the primitive arrangement of a ventral or superficial layer and a deep or dorsal layer. These two are connected at their extremities by means of the two buttresses at the mesial and lateral aspects of the nuclear formation.

The superficial layer corresponds closely with the surface of the pons, expanding into the lateral buttress and coming into close contact with the ventrolateral angle of the reticular formation. The mesial buttress is an extensive mass of gray matter lying in contact with its fellow of the opposite side and fusing dorsally with the deep layer of the pontile nuclei. The union of the two nuclear masses across the midline is so extensive as to form a shield-like structure, overlapped on either side by the ventral prolongation of the superficial layers of the pontile nuclei. The internal, lace-like arrangement of the nuclei is prominent in the chimpanzee. Massive strands of nuclear material pass transversely between the two buttresses and present branch-like forms which pass to the lateral and mesial buttresses. These strands of gray matter serve to break up the pallio-spinal and pallio-pontile tracts into a great number of smaller bundles. The pontile nuclei are continued upward into the isthmus mesencephali and begin to disappear in their most lateral and dorsal region. Their disappearance from this region results in the coalescence of the constituent parts of the occipito-parieto-temporo-pontile fibers. The superficial layer gradually diminishes. The mesial buttress then continues upward alone for a short distance, finally merging with the indifferent interpeduncular gray matter. The deep layer of the pontile nucleus extends cephalad and at length merges with the substantia nigra. The deep layer of the pontile nuclei is in contact with the ventral surface of the reticular formation mesially and laterally. In the mid-pontile region a separation is brought about by the development of the trapezoid body.

Large spaces appear on the lateral surface of the superficial layer of the pontile nucleus, from which emerge the bundles of the pontocerebellar fibers. This breaks up the lateral surface of the pontile nuclei into an irregular appearing surface, quite unlike the relatively smooth surface presented by the superficial layer in the lower primates in which the pallial connections with the cerebellum are relatively meager.

The Vestibular Complex

This nuclear mass makes its appearance in the caudal ventricular portion of the medulla where it first assumes recognizable proportions as a small triangular mass. It is situated between the floor of the fourth ventricle and the dorsomesial aspect of the nucleus of Goll. In this region the vestibular complex is represented by the nucleus of Deiters. Increasing steadily in lateral and ventrodorsal extent this nucleus progressively separates the nucleus of Goll from the lateral wall of the fourth ventricle. Above the upper limit of the nucleus of Goll the lateral surface of Deiters' nucleus comes into relationship with the upper portion of the nucleus of Burdach. Laterally the nucleus of Deiters has a definite ventral prolongation, triangular in shape, which extends forward and lies in contact mesially with the lateral surface of the descending tract of the trigeminal nerve. In reconstruction the substantia gelatinosa trigemini is in close relation with, but separated from, the nucleus of Deiters by a cleft in which is lodged the descending root of the trigeminal nerve.

In the mid-ventricular region Deiters' nucleus gradually begins to diminish in size and is replaced by the triangular nucleus of Schwalbe situated somewhat dorsal and slightly mesial to the Deitersal nucleus. This nucleus continues upward to the mid-pontile level where it gradually diminishes in size and then disappears. The triangular nucleus is covered by the dorsal cochlear nucleus which lies immediately subjacent to the subependymal gray matter forming the floor of the fourth ventricle.

Above the opening of the lateral recess the nucleus of Bechterew appears in the extreme dorsolateral angle of the tegmentum extending into the lateral wall of the ventricular cavity. The entire vestibular complex extends cephalically as far as the upper limit of the substantia gelatinosa trigemini. Its ventral prolongation passes deeply into the tegmentum of the metencephalon, approaching closely to the transverse plane of the neuraxis.

The Cochlear Complex

The cochlear complex consists of the ventral and the dorsal nuclei which are connected by strands of nuclear material. The ventral cochlear nucleus is relatively massive but not augmented in proportion to the absolute increase in the amount of nuclear material of the brain stem. By comparison the relative mass of gray matter would seem to be less than that found in some of the lower forms such as the Macacus rhesus and the Cynocephalus babuin. The central cochlear nucleus is arranged in the usual fashion, more or less trough-like in shape, enveloping the entering cochlear root on its caudal, lateral and cephalic surfaces. The dorsal nucleus is relatively extensive and lies directly in contact with the subependymal gray matter in the floor of the fourth ventricle. It is traversed by a number of the fibers of the secondary cochlear tracts which have already received relay in the ventral cochlear nucleus and are passing across the floor of the fourth ventricle.

The Colliculi

These masses of gray matter in the tectum of the mesencephalon represent a relatively massive accumulation of nuclear material. The inferior colliculus appears as a specialization in the dorsal extension of the mesencephalic reticular formation which supports the colliculi at their lateral extremities. Dorsally the inferior and superior colliculi are continuous with the indifferent gray matter lying in the midline. Each colliculus is connected across the midline by the decussating fibers respectively of the inferior and superior collicular commissures. These decussating fibers support the dorsal gray matter and produce a definite cleft between this element and the dorsal surface of the central gray matter.

Caudally and laterally the entrance of the lateral fillet into the area immediately subjacent to the inferior colliculus is clearly shown in the reconstruction. The inferior colliculus is separated from the superior colliculus by the intercollicular sulcus which is occupied by a dorsal extension of the mesencephalic reticular formation and a similar extension serves to separate the superior colliculus from the dieneephalon.

The Substantia Nigra

The substantia nigra appears in its usual situation, developing from the dorsal layer of the pontile nucleus from which it seems to be derived. It is supported by the dorsal layer and, to a less extent than is the case in the lower forms, by the lateral and mesial buttresses. It is marked ventrally by the longitudinal fibers of the pallio-spinal and pallio-pontile systems. It merges mesially with the interpeduncular gray matter, pierced at this point by the emerging fibers of the oculomotor nerve. Laterally it presents the nuclear specialization which has been found regularly to take place in this part of the substantia nigra in the lower primate forms. Laterally it comes into close relation with the mesial geniculate body, but does not make actual contact with this nuclear mass. Dorsally it is separated from the reticular formation by the circumferential fibers of this formation.

The Nucleus Ruber

The nucleus ruber is a large nuclear mass which is first encountered at a point near the mid-mesencephalic level. Here it appears as a rounded encapsulated structure amidst the decussating fibers of the superior cerebellar peduncle. It rapidly increases in size, occupying almost the entire mesial half of the mesencephalic reticular formation and extending upward into the diencephalon.

The Central Gray Matter

The central gray matter in the high cervical levels appears identical in form with the central gray matter of the human adult. It is disposed as a quadrilateral mass surrounding the central canal of the spinal cord.

As the oblongatal nuclei develop and the inferior extremity of the floor of the fourth ventricle is approached the central gray matter passes in a dorsal direction, sending backward a thin lamina toward the dorsal periphery of the neuraxis. As this dorsal migration takes place the quadrilateral form of the central gray matter undergoes a change. It becomes flattened out and then, as the fourth ventricle opens, the entire extent becomes disposed in a single layer extending from side to side. A thin layer of gray matter remains in the lateral wall and the roof of the fourth ventricle as the subependymal gray matter.

In the lower part of the fourth ventricle the prominence of the hypoglossal nucleus is easily identified close to the midline. Somewhat above and lateral to this is a triangular depression which corresponds to the underlying dorsal nucleus of the vagus.

The ventricle as it opens becomes more extensive from side to side. In the mid-ventricular portion the markings become more evident, showing the outline of such underlying nuclear masses as the vestibular and cochlear complexes. Above the mid-point of the ventricle as it begins to narrow toward the aqueduct of Sylvius a marked median eminence appears on both sides of the midline, representing the eminentia abducentis and the subventricular course of the seventh cranial nerve.

Above the lateral recess, the walls of the ventricle rapidly approach each other and the formation of the aqueduct of Sylvius results in the development of a massive central gray matter encircling the ventricular cavity. In the isthmus the nucleus of the fourth cranial nerve appears in this ventral prolongation of the central gray matter. With but little distinction between the nucleus trochlearis and the nucleus oculomotorius above it, the latter nucleus occupies this same ventral prolongation. As the diencephalon is approached this prolongation becomes more extensive until it is continuous with the interpeduncular gray matter, thus forming a complete griseal lamina between the midline and the mesial surface of the red nucleus.

The central gray matter continues upward to the junction of the mesencephalon and the diencephalon, where it becomes continuous with the subependymal gray matter of the third ventricle. It merges with the ill-defined mesial group of the diencephalic nuclei, the epithalamic structures and the hypencephalic region.

Chapter XXI

TROGLODYTES GORILLA, ITS BRAIN AND BEHAVIOR

Its Position among the Primates; Measurements and Brain Indices; Surface Anatomy of the Brain; Internal Structure of the Brain Stem in Cross Section

Appearance of the Gorilla

THE gorilla, in point of size, when standing upright, is nearly as tall as the average man. Its recorded measurements give it a height of five feet two inches to over six feet. Its body is stout and large, its legs short and its arms long. The tips of its fingers reach to about the middle of the leg below the knee. Its huge grisly head, flat, broad nose, prominent muzzle, large mouth, very large canines, and protruding ears which are uncovered by hair, all contribute to give the animal a terrifying appearance upon which is based much of its generally accepted reputation for ferocity. In some instances the full-grown adult attains the great weight of between three hundred and four hundred pounds. This fact, added to its awe-inspiring locomotion when it rises upon its hindlegs and stretches forth its tremendous arms, has made the gorilla known as the most savage of all beasts, and at the same time one of the most dangerous of all the enemies of man.

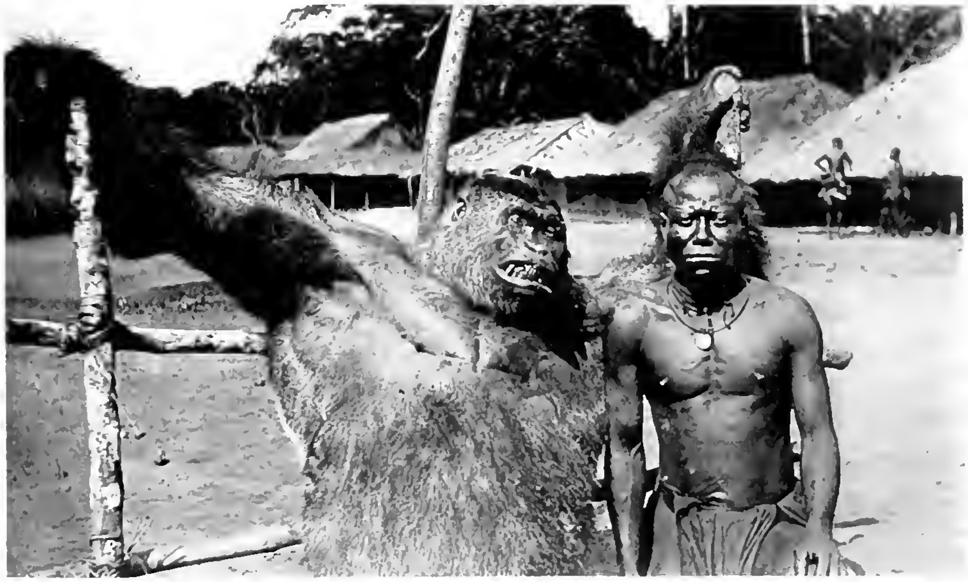
The hands are large and wrinkled, thickly covered with hair on the back, but the palmar surfaces are without hair and present cutaneous rugae, no doubt in the interest of amplifying the areas for sensory receptors. The thumb is somewhat short for the size of the hand but is thick and bears a broad nail. The great toe is opposable, large and flat, and the proximal phalanges of the second, third and fourth toes are united by a web.

The animal's body, as well as the head up to the brow-line, is covered with shaggy hair. The skull is massive and the eyes surmounted by protruding supra-orbital ridges. A heavy sagittal crest of bone extends from the frontal to the occipital region, giving attachment to an exceptionally large temporal muscle whose presence, together with a short, thick neck, imparts

Courtesy, American Museum of Natural History

FIG. 275. GORILLA GROUP, FROM THE AMERICAN MUSEUM OF NATURAL HISTORY. THESE SPECIMENS WERE OBTAINED AND PREPARED BY THE LATE MR. CARL AKELEY IN HIS LAST GORILLA HUNT.

so much of the appearance to the animal upon which its reputation for pugnacity depends. It is true that the heavy head, short thick neck and tremendous arms create the impression of a peculiarly efficient fighting machine,



Courtesy, American Museum of Natural History

FIG. 276. LARGE MALE GORILLA KILLED IN THE AFRICAN CONGO.

which, however, has one great inherent weakness in the imperfect development of the legs and feet. The animal is able to assume the upright position and walks thus in an awkward manner, using the great arms to aid in balancing. In the main, however, it goes upon all fours, particularly when desirous of making speed through the underbrush or climbing among the trees. It rises upon its hindlegs largely for purposes of inspection, in order to make a survey of the surrounding territory through which it may be traveling. Whether it assumes the erect posture when charging to an attack, or simply stands upright in combat in order to permit the freer use of its great power in the upper extremity, is a question which has not yet been decided.

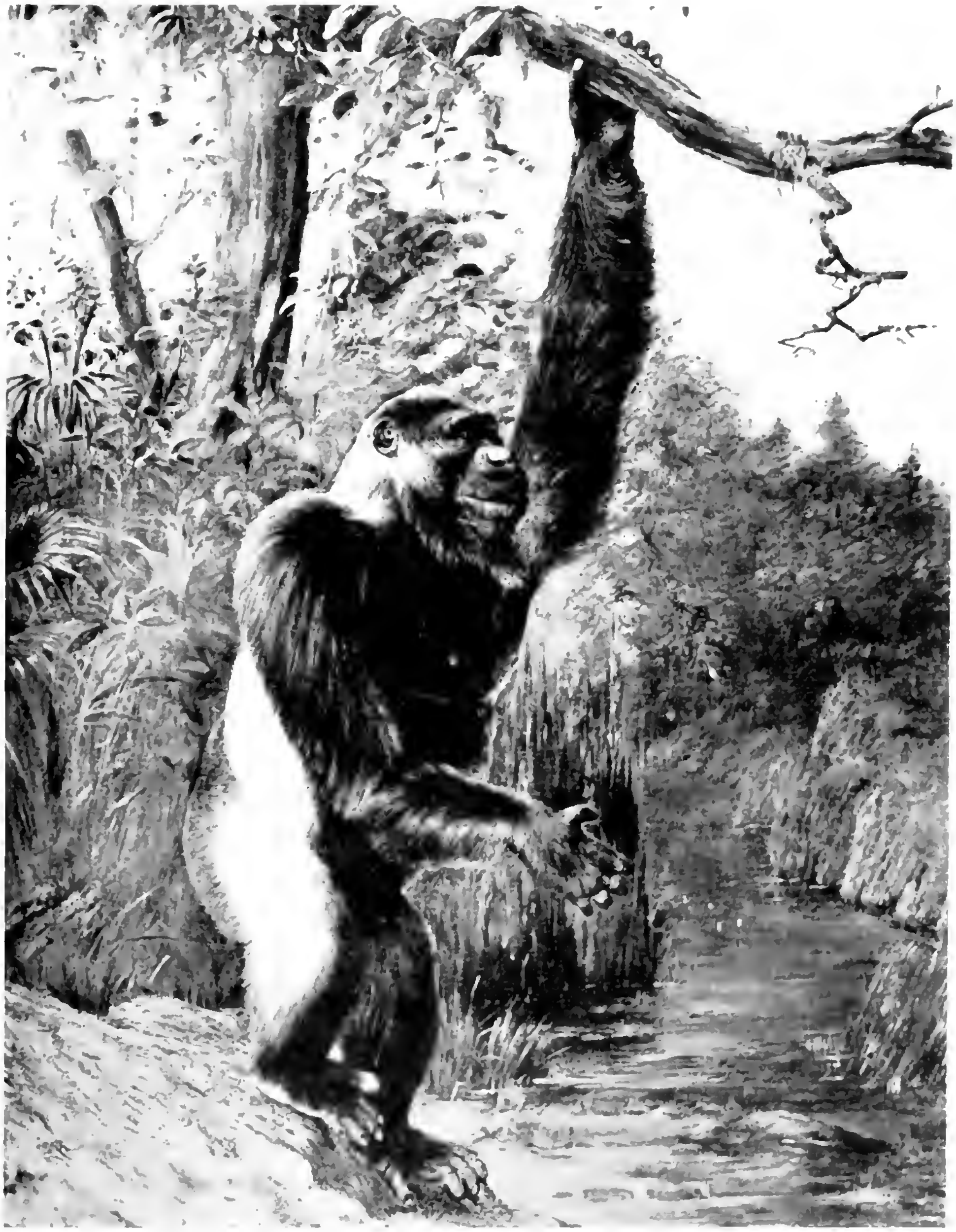
Habits of the Gorilla

Some six or seven species and subspecies of gorilla have been identified; although much is still to be desired in the matter of exact classification. The animal here described is Gorilla gorilla, also known as Troglodytes gorilla. Its habitat is in the Gaboon of West Africa. This gorilla is also known to inhabit regions in the southern and northern Camaroon of West Africa, near the border of the French Congo. It also has been discovered in localities about the Belgian Congo.

Ancient rumor spread abroad the report that there lived in Africa a huge ape of most ferocious and savage disposition. Around this rumor fabulous stories concerning the great strength of this monster as well as its predatory, man-like behavior were soon built up. Indeed, gorillas were first spoken of as wild, hairy men. It was Hanno who appears to have been the first to encounter them during his famous voyage to the Pillars of Hercules. Coming upon a group of these wild people he was able to capture three of the women but all of the men managed to make their escape. The females, however, fought so savagely that it was necessary to kill them. Their skins were preserved and brought to Carthage where they were placed in the temple of Juno and were still there when that city was destroyed. The noted explorer, Paul Du Chaillu, in his "Adventures in Equatorial Africa," describes the gorilla as gregarious, going in companies of eight to ten. Sometimes when the older males become superannuated, they live solitary lives apart from these small communities, and when thus grown old, appear to be actually grizzled with age, their hair becoming almost white.

DU CHAILLU'S DESCRIPTION OF THE GORILLA'S HABITS

Du Chaillu probably was the first European to kill a gorilla in its native forest. His description of their habits is no doubt more accurate than it was at first believed to be. It was his opinion that the gorilla did not, as often



From "A Review of the Primates." By D. G. Elliot.

FIG. 277. GORILLA GORILLA.

Courtesy, American Museum of Natural History

FIG. 2-8. BRONZE STATUE BY FREMIER.

Based on the legendary account of the gorilla's attacks upon man in which he is said to have captured native women and carried them off into the forest. This legend was subsequently proved by Paul Du Chaillu and other explorers to be wholly unfounded. It is such a misrepresentation of the known facts that the American Museum of Natural History will not permit the exhibition of this bronze.

Courtesy, New York Zoological Society

FIG. 279. JOHN DANIEL IN AN AMIABLE ATTITUDE, ENTIRELY CONTROVERTING THE GORILLA'S REPUTATION FOR FEROCITY.

claimed, lurk in trees by the roadside to drag up with its great arms the unsuspecting passer-by, later to choke him to death. He discredited the statement that these animals attack the elephant and beat him to death with sticks, or that they carried off women of the native villages to devour them in the depths of the forest. He did not even believe that the gorilla built itself a house of leaves and twigs among the trees, and denied that it ever became gregarious to the extent attributed to it in many stories. It did not settle in large communities nor did it assemble in great numbers to make concerted attacks upon men who established their habitations near the confines of its forest home. Du Chaillu observed that the animal inhabited the loneliest portions of the dense African jungles and seemed to prefer deep, wooded valleys and rugged heights. The high plains covered by large boulders were also its favorite haunts. In general, a plentiful supply of water is found in such territories.

The animal appears to have a roaming tendency which may be induced by the necessity of obtaining food. It is rarely found in the same place two days in succession. It wanders from region to region over long ranges in search of such food as pineapple leaves, berries and other vegetable matter of which the animal is a large eater. Wild sugar cane has been mentioned among the things upon which it subsists, as well as nuts whose hard shells are cracked by the powerful jaws. The animal sleeps sitting upon the ground with its back against the trunk of the tree, and when full-grown seldom ascends high among the branches. The young sleep in the trees and possibly the females may occasionally do so. In spite of their reputation for ferocity, the gorillas are in reality shy, and the female especially will run to shelter at the first sound of alarm, carrying her young with her if she has one. The male is not so precipitate in his flight. He rises upon his hindlegs for a moment, showing his savage visage in the underbrush. Then, glaring at the intruder, he begins to beat his breast with his closed fists at the same time lifting up his head and uttering an awe-inspiring roar. This sound begins at first with several loud barks like those of a dog, and then changes to a guttural roar which is repeated with redoubled power causing echoes in the forest which reverberate like distant thunder. Du Chaillu says that the horror of the animal's appearance at this time is beyond description. It seems as a monster in a nightmare and so impossible a piece of hideousness that were it not for the danger of its savage approach the hunter might imagine himself in an ugly dream.

AKELEY'S EXPERIENCES WITH THE GORILLA

The gorilla's gait is more of a waddle from side to side, its hind legs being short and thus inadequate to support its huge body properly. While swinging his arms to balance himself, his great trunk moves backward and forward, adding to the gruesome horror of his appearance. When approaching to the attack, the features are distorted by hideous wrinkles, the sharp lips drawn back to reveal long fangs in a powerful jaw by which a human limb could easily be crushed. It is not difficult to shoot a gorilla, however, and thus render its savage attack all too easy of restraint. In fact, Akeley, the noted African explorer, said in reference to hunting the gorilla that there is no greater difficulty in shooting this sort of game than there would be in killing a defenseless, crippled woman. Far from being sport, it is most distasteful, indeed an atrocity closely akin to murder. It was due to Akeley's good offices and efforts that the King of Belgium set aside a large territory in the Congo as a Gorilla Sanctuary in which all hunting of this animal is prohibited. Here, Akeley hoped, a biological station might be ultimately established for further study of the gorilla's behavior. He believed it would be possible to gain a footing on close and intimate terms with this great anthropoid which, in spite of its vaunted reputation for ferocity is, in his opinion, so timid that it will require years of careful cultivation to establish the necessary feeling of friendly relations. Akeley's recognition of the gorilla as a timid and retiring anthropoid, with none of the atrocious characteristics for which he has so long been famed, is ground for the expectation that in time this fast disappearing offshoot of the prehuman stock may furnish its full quota of testimony concerning the evolutionary process in its relations to the derivation of man.

JOHN DANIEL I

In adult life the animal is quite untamable, although if captured young, as much may be done with it as with any of the other primates in captivity. The following account of a gorilla's life in civilization, as given by Miss Alyse Cunningham, of London, testifies to this fact. This record is based on observations made by Miss Cunningham of the young gorilla called "John Daniel." At first she had no fancy for this animal. She in fact was affected by rather a dislike for anything in the shape of a monkey or ape. But she soon became interested in the young gorilla and took his education seriously in hand. The animal was presented to her by her nephew, Major Penny, who was much interested in primates, and bought the gorilla with the idea of seeing how much mentality could be developed in this highest of the anthropoids. John Daniel was captured when very young, in the French Gaboon country, and came to England when he was about three years of age. At this time he was suffering from a rachitic condition and had also contracted a severe influenza through which Miss Cunningham nursed him and so successfully cared for him during the next three years that he reached the weight of 112 pounds and the height of 3 feet 4½ inches. Meanwhile he acquired much of the adaptation necessary to fit him as an interesting, if rather unusual member of the household. To Miss Cunningham we are indebted for excellent observations which indicate the extent to which this anthropoid may be trained and educated. Her impressions have given a new idea as to the disposition and teachability of the gorilla.

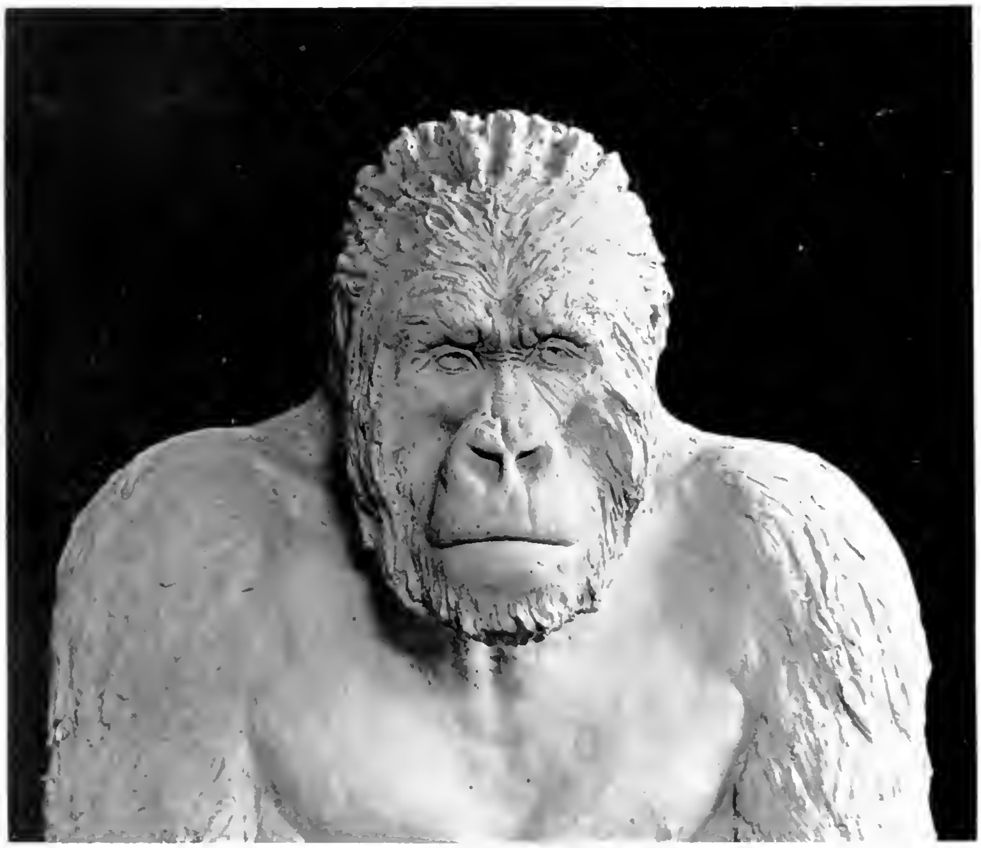
The young gorilla immediately showed marked emotional reactions which caused some difficult complications in the household. If he were left by himself at night he would shriek from fear and loneliness. Miss Cunning-

Courtesy, American Museum of Natural History

FIG. 280. SIX-YEAR-OLD GORILLA, JOHN DANIEL.

[See Text p. 632]

ham therefore treated him as she would a child, and had her nephew place his bed every night in the room adjoining the cage of the gorilla. As a result, John became quite happy, at once began to grow and put on weight. He was next taught to be clean in his habits, and by a series of rewards and punishments at the end of six weeks was thoroughly house-broken. He was then taken out of his cage and allowed the freedom of the house. Thereafter, he ran upstairs to the bathroom of his own accord, turning the knob of the door of whatever room he was in, and also opening the door of the bathroom. He showed great fastidiousness in the matter of diet, although he much preferred stealing his food to having it given to him. He appeared to think himself



Courtesy, American Museum of Natural History

FIG. 281. PLASTER CAST OF AN OLD MALE GORILLA TAKEN IN THE LAST GORILLA HUNT OF MR. CARL AKELEY.

more clever in such transactions and was averse to considering himself the recipient of favors from others. He showed a strange disposition to avoid all food which had been exposed to the air for long. He was particularly fond of oranges and apples, but would not eat these or any other fruit if they had been cut a few hours. He had what almost amounted to a passion for eating roses. The more beautiful they were the more he liked them, although he never would eat faded roses. He liked nibbling at twigs and also eating green buds in the spring. The animal never cared much for nuts of any kind except walnuts. His actions with a cocoanut were rather amusing. He knew that it had to be broken and would try to break it by throwing it upon the floor. Failing in this, he would bring it to one of the members of the family and try to make his desire understood. If given a hammer he would try to use it on the nut; and then, being unable to accomplish his purpose, would present the hammer and the cocoanut to someone to help him out. He very well understood the use of hammers and chisels, but was never encouraged to attempt anything in the line of carpentry out of general respect for the household furniture.

John Daniel was particularly fond of having people come to visit him at his home. Whenever there were visitors he would show off like a child. It was his custom to take the visitor by the hand and lead him round and round the room. If he saw that a person was at all nervous, he enjoyed running past him and giving him a smack on the leg, after which he would grin at the visitor's displeasure. His table manners were rather exceptionally good. He always sat at the table, and whenever the meal was ready would pull up his own chair to his place. He did not care to eat great quantities, but he especially liked to drink water from a tumbler. He always took afternoon tea of which he was very fond, and then would eat a thin slice of bread with plenty of jam. He always liked coffee after dinner. In general he was the least greedy of all animals that had come under the observation of his owners. He would never snatch anything and always ate slowly. He was accustomed to drink large quantities of water which he would get himself whenever he wanted it, by turning on a tap. Strange to say, he always turned off the water when he had finished drinking.

John Daniel seemed to think that everyone was delighted to see him, and for this reason he would stand on the window sill and throw up the shade. In a short time a large crowd collected to watch him in his position at the win-

Courtesy, New York Zoological Society

FIG. 282. YOUNG GORILLA, JOHN DANIEL, FROM A MOTION PICTURE TAKEN TO SHOW THE CHARACTERISTIC BREAST-BEATING ACT OF THE GORILLA.

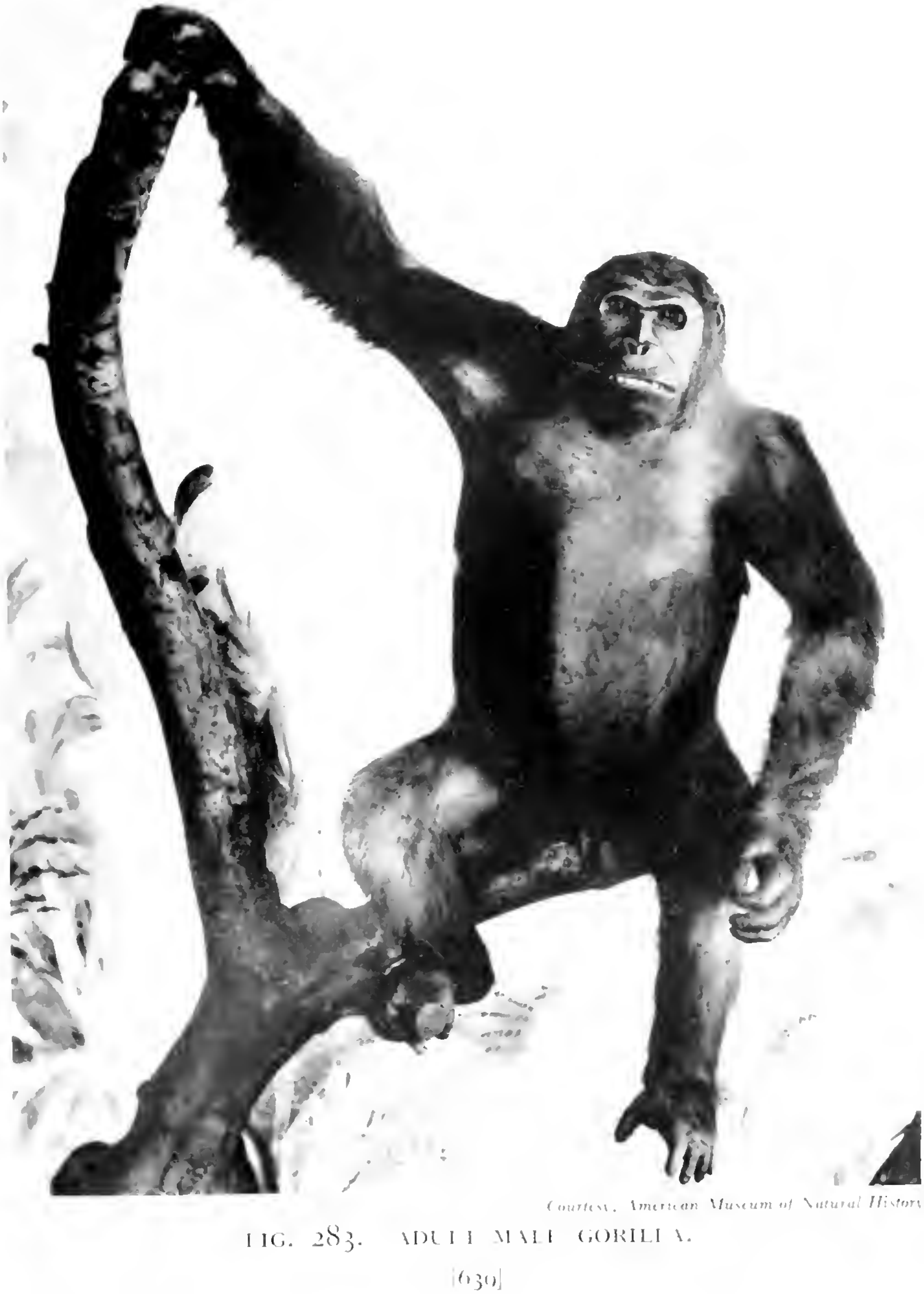
dow. When it appeared to him that the crowd was of sufficient numbers, he would often pull the shade deliberately down in their faces, and run away shrieking with laughter, seeming to feel that he had perpetrated a huge joke upon the curious audience outside.

He was especially attached to Miss Cunningham's little three-year-old niece who often came with her mother to stay in the house. John Daniel and she played together by the hour. He seemed to understand just what she wanted him to do. If she cried for any reason, when her mother came to pick her up, the gorilla would always try to nip the mother and give her a slap with the full weight of his hand, apparently thinking that she was the cause of the child's tears. One day Miss Cunningham was dressed for going out and John Daniel wished to sit on her lap. It chanced that her dress was a light one and she pushed him away saying she feared that he might soil her gown. He at once lay on the floor and cried like a baby for a moment; then he rose, looked around the room, found a newspaper, spread it out on Miss Cunningham's lap and climbed up upon it. This was quite the cleverest thing that he had ever done, and those who saw it said that they would not have believed it had they not themselves been present.

The gorilla apparently could stand much cold and he often would go on the roof in freezing weather. This he did not seem to mind so long as he could come into a warm room when he wanted to; then he would go straight to the fire, rub his chest and sit down with his feet on the fender. Exercise was essential to keep him in health and he got much of this by playing hide-and-seek with Major Penny in the morning before breakfast and in the evening before dinner. The major would run up and down the stairs, in and out of all the rooms. The game appeared to delight the gorilla who would giggle and laugh while being chased. He was very cautious, however, never to enter a dark room without first turning on the light. It was his habit to retire each night at eight o'clock. He had his own little room adjoining that of Miss Cunningham's nephew where he had a spring bed of his own with blankets. He would get out of it at night by himself, go back to bed and pull the blankets up over him quite neatly. The thing he enjoyed most was to stand on the top rail of his bed and jump on the springs, head over heels, just like a child.

John Daniel was never taught any tricks. He simply acquired knowledge himself. He was taken in summer by train to the family's cottage in the country, occupying his seat in the railway coach as an ordinary passenger without even a chain around his neck. He seemed to be much afraid of the fields and the open country, but was happy in the garden and the woods. Full-grown sheep, cows and horses he seemed to fear; but colts, calves or lambs afforded him much amusement and he was greatly interested in them. It seemed to those who cared for him that he recognized youth and was sympathetically drawn to it. He became so attached to the family that if left alone he would make a great noise, shrieking and crying. This tendency increased so that after three years it was necessary to make some other arrangements for him. Due in large measure to a misunderstanding which his owners have always regretted, John was sold to a circus, transported across the Atlantic to New York, where, after a month's separation from his friends and protectors, during which time he refused to take food and showed other signs of real homesickness, he died in the tower of the old Madison Square Garden, in April, 1921. The skeleton and taxidermic preparation of this remarkable gorilla which contributed so much to our knowledge and better understanding of the great troglodyte anthropoids may be seen among the gorilla collection of the American Museum of Natural History. Most of the serial sections introduced in this work, illustrating the brain stem of the gorilla, were obtained from John Daniel the First.

It may be added as a note to this instructive history of what appears to be the first gorilla raised under the conditions of such intimate domestic life, that Miss Cunningham has become so much interested in the species as to secure another young gorilla which she called John Daniel the Second. John Daniel the First was a little over six years old when he died. The present specimen of this species possessed by Miss Cunningham is of about the same age. In many respects, these two great apes correspond in their emotional reactions and their susceptibility to training. John Daniel the Second is, perhaps, a less likable individual and has a disposition more in keeping with the ancient reputation of the great anthropoids.



Courtesy, American Museum of Natural History

FIG. 283. ADULT MALE GORILLA.

In any event, the writer had the honor about a year ago of being invited to take afternoon tea with John Daniel II who was then residing in a fine suite of rooms in a fashionable New York hotel. On this occasion the host was

Courtesy, American Museum of Natural History

FIGS. 284 AND 285. CASTS OF HAND AND FOOT OF THE GORILLA, JOHN DANIEL.

found seated in a comfortable and thoroughly human fashion upon a chair, surrounded by quite a gathering of scientific authorities, interested from one point of view or another in the behavior of anthropoids. With much gravity and apparent enjoyment, he drank from a cup of tea. Presently he indicated a desire for more of this beverage of which he would drink large quantities if permitted to do so. During the course of the usual amenities of the occasion, when, for the moment, the gorilla was not the actual center of attention, he suddenly dashed across the room with unbelievable swiftness and attacked one of his visitors with repeated, rapid blows of both fists, in the neighborhood of the solar plexus; then, with equal celerity, he hopped over the foot of the bed from which point of vantage he watched the discomfiture of his guest and prepared for further mischief. A moment later, when again less sharply watched, he suddenly hurled himself with his full weight,

Courtesy, American Museum of Natural History

FIGS. 286 AND 287. CASTS OF HAND AND FOOT OF THE GORILLA, JOHN DANIEL.

quite in the most accepted football style, against a distinguished Professor of Zoology who in consequence was thrown from his chair. In the intervals between these presumedly playful diversions, the gorilla sat quietly in his chair with a real semblance of proper decorum and apparently quite indifferent to the company. But in spite of his innocent demeanor, the very placidity of his manner gave rise to suspicions that he was casting about for the next piece of mischief which he might perpetrate. There was such a degree of roughness and such sudden development of strength in the playfulness of this juvenile gorilla, as to afford some idea of the terrific power which these animals must possess when full-grown. Before departing for London, John Daniel the Second inflicted a serious wound with his teeth upon the hand of one of his attendants.

The prospect of Mr. Akeley's proposed biological station in Africa for

Courtesy, American Museum of Natural History

FIGS. 288 AND 289. CASTS OF HAND AND FOOT OF AN ADULT MALE GORILLA.
LEFT. Palmar surface of the hand showing distinct humanoid tendencies.
RIGHT. Plantar surface of the foot showing broadening of the heel, migration of the great toe and shortening of the lesser toes in adaptation to semi-terrestrial life.

the study of the massive anthropoid in his native jungle is no doubt inspiring, yet if one may hazard an opnion from the somewhat superficial and passing acquaintance with the half-grown animal under most favorable social influence, it will be a long time ere others than the most hardy human adventurers seek fraternizing communion with the giant anthropoid even in the safeguarded regions of the gorilla sanctuary.

Courtesy, American Museum of Natural History

FIGS. 290 AND 291. CASTS OF THE HAND AND FOOT OF THE GORILLA, JOHN DANIEL.

TOP. Cast of the plantar surface of the foot of the gorilla, John Daniel, showing marked humanoid tendencies in the distal migration of the great toe, the broadening of the heel and shortening of the toes.
BOTTOM. Cast of the dorsum of the hand of the gorilla, John Daniel.

MEASUREMENTS AND INDICES OF THE GORILLA

Total length of the skull	230 mm.
Occipito-nasal length	135 mm.
Intertemporal width	98.1 mm.
Breadth of the brain case	92 mm.

The dimensions of the brain are:

Longitudinal	123 mm.
Transverse	87 mm.

The average weight of the brain in the full-grown adult enclosed in the dura mater and pia mater is 450 gms., without the dura mater, 445 gms

The following weight and water displacement values were obtained from the measurement of the adult female gorilla, Number 4, of the Akeley African expedition of 1921.

Volume of the brain:

Forebrain	364 c.c.
Midbrain	5 c.c.
Hindbrain	60 c.c.
Total water displacement	429 c.c.

Weight of the brain:

Forebrain	359 gms.
Midbrain	5 gms.
Hindbrain	59.5 gms.
Total weight	423.5 gms.

On the basis of these figures, encephalic indices were computed:

Forebrain index	84 per cent
Midbrain index	2 per cent
Hindbrain index	14 per cent

Surface Appearance of the Brain of Gorilla

Fissures and Lobes

The appearance of the brain in gorilla closely resembles that in man. In size, however, its dimensions are a little less than one-half of the adult human male. Its general outline and fissural patterns are conspicuously humanoid. The design of the lateral surface of the hemisphere is distinctly quadrilobular, with three well-defined fissures separating four equally well-defined lobes. The fissure of Sylvius separates the parietal from the temporal lobe; the fissure of Rolando, the parietal from the frontal lobe; and the sulcus simiarum, the occipital from the parietal lobe. The latter fissure may be traced to the mesial surface of the hemisphere where it occupies a position identical with that of the parieto-occipital fissure in the human brain. The fissure of Sylvius has all of the appearance characteristic of the corresponding sulcus in man; while the Rolandic fissure has an even closer correspondence to its human counterpart. The entire region comprised within the Rolandic, Sylvian and simian sulci is richly convoluted and in it are all of the landmarks of the similar temporo-parietal area in man. As in most of the primates, this region is highly convoluted, since it develops in response to specializations in somesthetic sensibility and the special sense of hearing. In the occipital lobe there is a marked degree of convolution, while the fissural pattern is in many respects laid down as though in strict accordance with a human prototype. This is true both of the mesial and the lateral occipital surfaces.

More striking are the accessions to convolutional pattern and richness of fissural impression which occur in the frontal lobe. This feature distinguishes the gorilla's brain from the lower and intermediate primates, and gives it, at least to superficial inspection, predominance over the corresponding lobe in the orang and chimpanzee.

THE BASAL SURFACE

Certain features on the basal surface are equally important in their close correspondence to the human brain. The two characteristic concavities of

FIG. 292A. DORSAL SURFACE OF BRAIN, GORILLA.
[Actual Length 117 mm.]

this surface, both supra-orbital and cerebellar, show a marked decrease in prominence as compared with the lower and intermediate forms. The structure often denominated the interorbital keel of the frontal lobe has lost much of its prominence and approaches more closely the conditions observed in man. The entire orbital surface of the frontal lobe has in fact so altered its

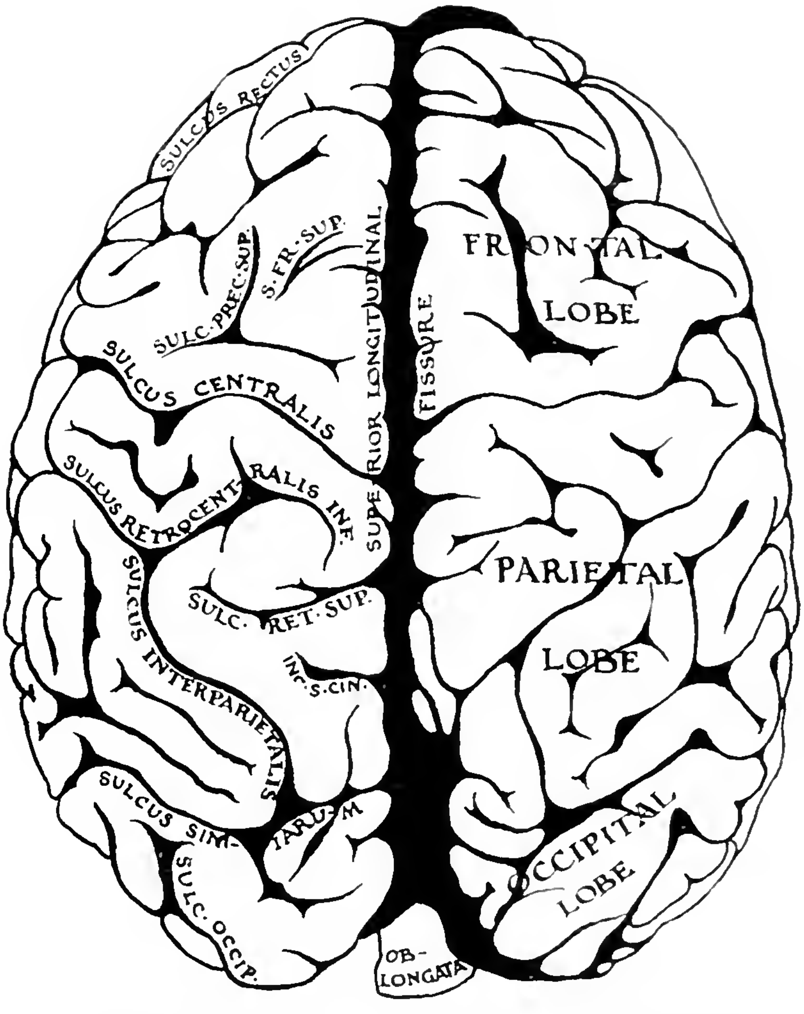


FIG. 292B. DETAILED DIAGRAM OF DORSAL SURFACE OF BRAIN, GORILLA. Key to Diagram, inc. s. cin., Incisura Sulci Cinguli; sulc. occip., Sulcus Occipitalis; s. fr. sup. Sulcus Frontalis Superior; sulc. prec. sup., Sulcus Precentralis Superior; sulc. ret. sup., Sulcus Retrocentralis Superior.

external configuration as, for the most part, to present a tendency toward convexity and is thus nearly devoid of the marked indenture so characteristic of lower species. The decrease in the orbital concavity is unquestionably due to progressive expansion of the frontal lobe. The fissural pattern of this orbital surface of the frontal lobe corresponds closely to that of man, while

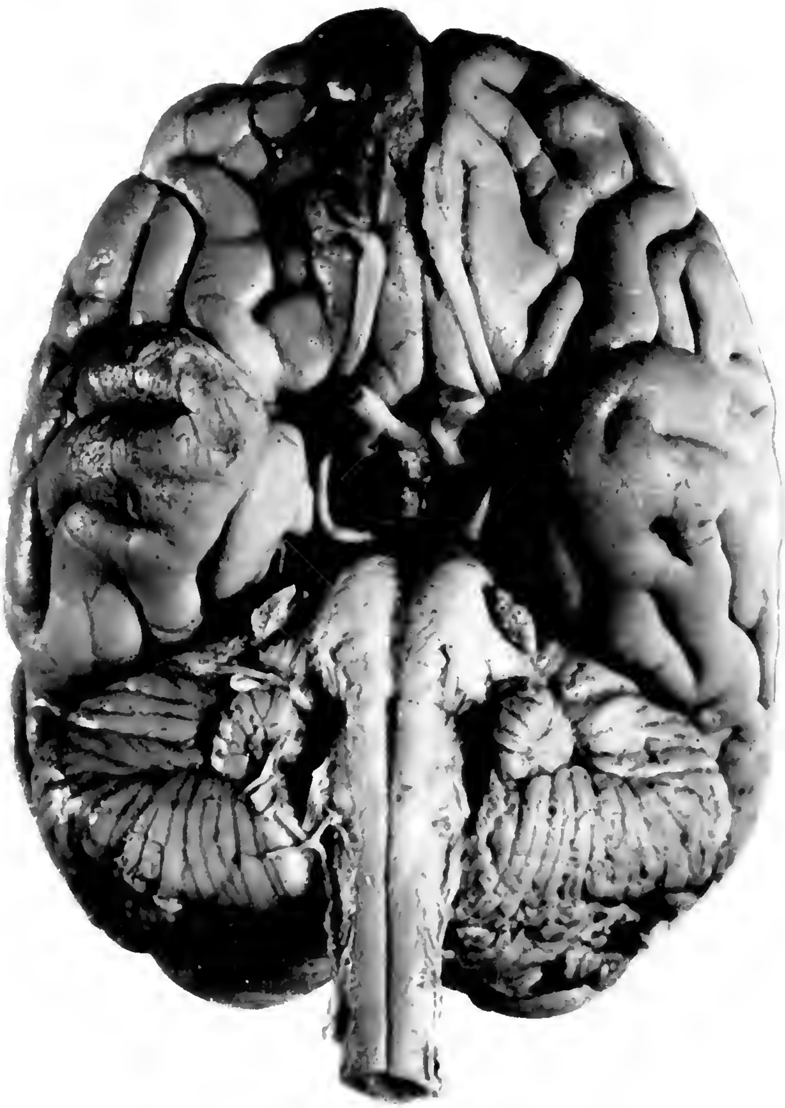


FIG. 293A. BASE OF BRAIN, GORILLA
[Actual Length 117 mm.]

the boundary between it and the lateral surface of the hemisphere is indicated, as in the human brain, by an anterior extension of the Sylvian fissure.

Nothing of the human detail is lacking in this region of the brain, save that the features are all less impressively drawn and have a greater simplicity of outline.

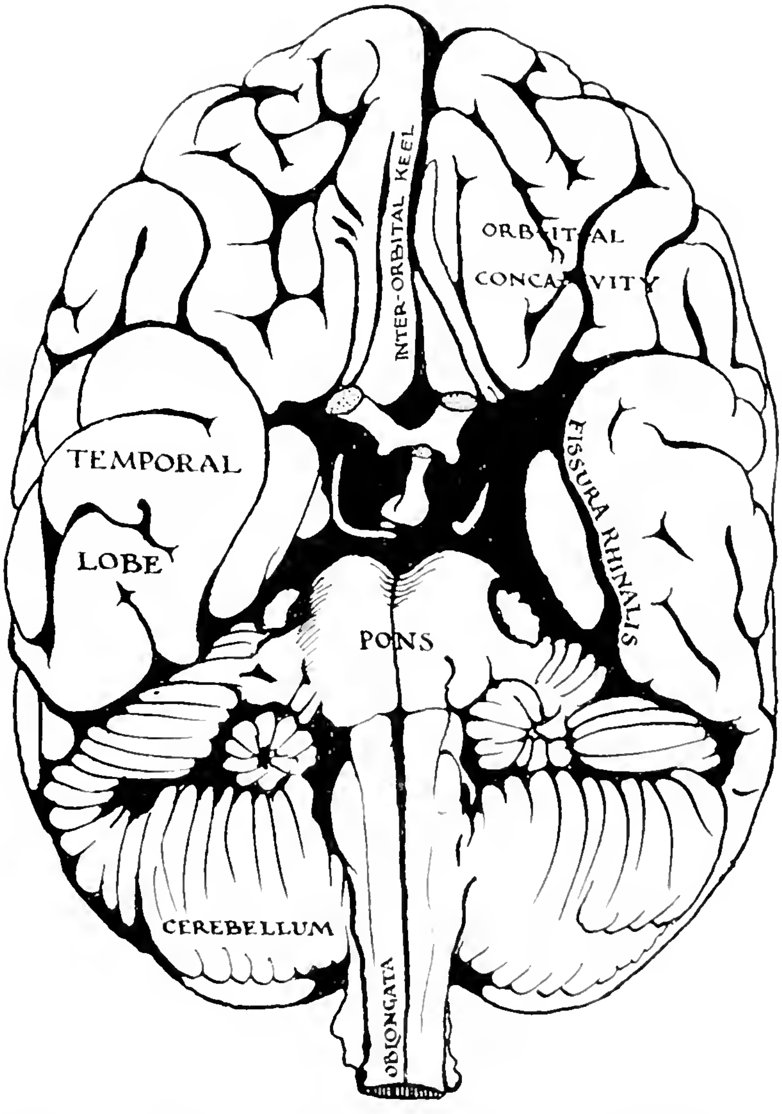


FIG. 293B. DETAILED DIAGRAM OF BASE OF BRAIN, GORILLA.

A marked characteristic of the primate brain is the detachability of the olfactory bulb and tract up to the trigonum olfactorium, in consequence of which these structures appear attenuated as compared with those of ungulates and carnivores. By retracting the olfactory bulb and tract, the gyrus rectus is brought to view as well as the medial olfactory fissure.

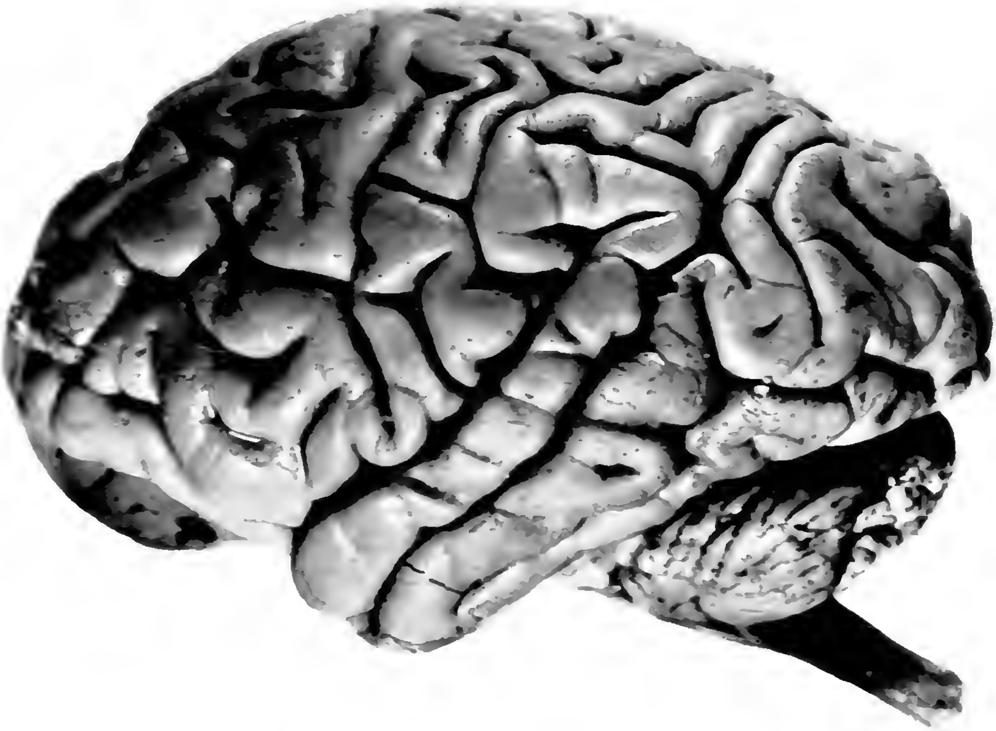


FIG. 204A. LEFT HEMISPHERE OF BRAIN, GORILLA.
(Actual Length 123 mm.

A second important character of the basal surface is the relation of the optic nerves and tracts to the chiasm. Their angulation, as is the case throughout the primate series, approaches the obtuse, the two optic nerves entering the chiasm at a little less than right angles, while the same angular relation obtains in the optic tracts. This condition is determined by the shortening of the nasal cavity and the protrusion forward of the frontal lobe into a position overlying the orbits.

In the occipital portion of the basal surface, the decrease in the cerebellar concavity is apparent. This is occasioned by the operation of two factors:

first, the expansion of the occipital region of the hemispheres in the interest of further enriching the visual fields and thus visual association; second, by a conspicuous expansion in the lateral lobes of the cerebellum. The decrease

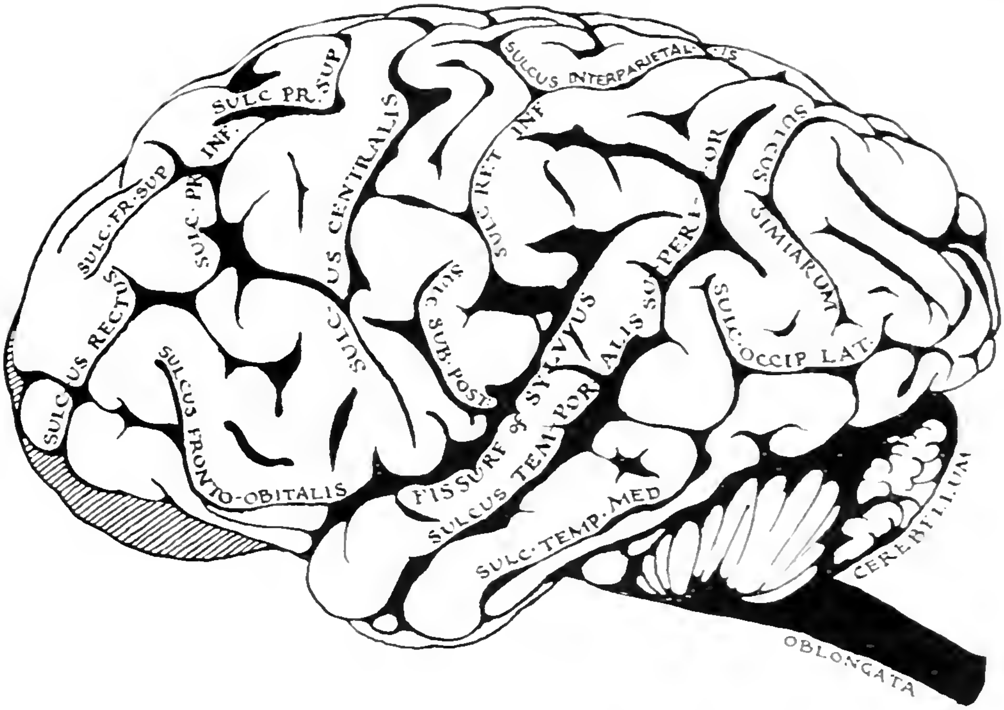


FIG. 294B. DETAILED DIAGRAM OF LEFT HEMISPHERE OF BRAIN, GORILLA. KEY TO DIAGRAM. SULC. FR. SUP., Sulcus Frontalis Superior; SULC. OCCIP. LAT., Sulcus Occipitalis Lateralis. SULC. PR. INF., Sulcus Precentralis Inferior; SULC. PR. SUP., Sulcus Precentralis Superior; SULC. RET. INF., Sulcus Retrocentralis Inferior; SULC. SUB. POST., Sulcus Subcentralis Posterior; SULC. TEMP. MED., Sulcus Temporalis Medius.

in the cerebellar concavity is shown particularly on the lateral aspect of the under surface. In but one region does this indenture bear any of its original prominence as seen in the lower primates. This is at a point near the midline just caudal to the splenium of the corpus callosum where a vestige of the former deep concavity is still apparent, the postsplenial fossa. In the main, the basal surface of the occipital lobe is assuming a tendency toward convexity and is rounding out its convolutions in such a manner that they pass over into the lateral surface without the sharp demarcation of the limiting ridge which surrounds the cerebellar concavity in lower species.

The fissures of this undersurface of the occipital lobe are identical with those of the human brain. The prominence attained by the tip of the temporal lobe is somewhat greater than that in the intermediate primates. It approaches more nearly to that of man. The uncus also is more pronounced both in its elevation and its demarcation.

All things considered, the convolutional and fissural patterns of the human and gorilla brain coincide so closely that were it not for the great disparity in size between the organs of these two species, the hemispheres of the one might be mistaken for those of the other.

THE CEREBELLUM

With regard to the cerebellum, equally striking advances have occurred. The entire organ has gained particularly in the region of the lateral lobes, where expansion has produced conspicuous alterations in certain features of its configuration. The tentorial surface is broader and flatter. The folial extension from the vermis to the lateral lobe is more pronounced for the reason that the superior vermis is less obviously delineated upon this surface. Its tendency to convexity in the vermal region has been largely lost due to expansion of the occipital lobes with a corresponding expansion in the lateral lobes of the cerebellum. Upon the tentorial surface in one place only is any degree of the former prominence of the vermis still retained; this is near its cephalic extremity in close relation to the inferior colliculi of the midbrain. Here the vermal portion of the cerebellum is considerably elevated and produces a corresponding depression between the occipital lobes, the post-splenial fossa. The tentorial surface is entirely overhung by the occipital lobes of the hemisphere, and the occipital notch, which in many lower forms is quite wide, is now much reduced in size.

The expansion of the lateral lobes of the cerebellum shows itself even more conspicuously upon the occipital surface of the organ where the bulging due to increase in size has produced two elevations. These rise above the inferior vermal portion of the cerebellum and cause it to sink deeply in a mesial depression, the vallecula. Lying in this position the inferior vermis appears relatively insignificant when compared with the two massive lateral lobes upon either side of it. If the lateral lobes are separated, two paramedian sulci may be discerned interrupting the continuity of the folial fissures as they pass from the vermis in the direction of either lateral cerebellar expansion. This submergence of the inferior vermis in the vallecular depression is a characteristic seen only in the higher anthropoids and man. It is one of the most significant indications of the expansion in the lateral lobes of the cerebellum. Nothing demonstrates more clearly the potential expansibility of the cerebellum than these lateral extensions. From this it appears that the rapidly increasing functional demand for augmented cerebellar control is made, not upon the primordial and more rigidly fixed central portion of the organ, but upon those plastic extensions of it which constitute the lateral lobes. The expansion of these cerebellar portions, in conjunction with simultaneous expansion of the cerebral hemispheres, indicates the fundamental nature of the bond existing between these two structures.

The petroso-ventricular surface of the cerebellum shows no great variation in its adjustment to the petrosal portion of the temporal bone and the roof of the fourth ventricle. At the cerebello-pontile angle there is a fairly well-defined but not conspicuous flocculus. The other markings correspond to all of the lower forms. This surface, therefore, represents a phyletically more fixed region than is the case with either the tentorial or occipital surface.

THE BRAIN STEM

THE OBLONGATA. The external appearance of the brain stem in gorilla gives the impression of an increasing definition in the outlines of all important features. Upon the ventral aspect of the oblongata are two pronounced elevations, one on either side of the ventromesial fissure, the long pyramids, in turn separated from two more laterally placed eminences, the

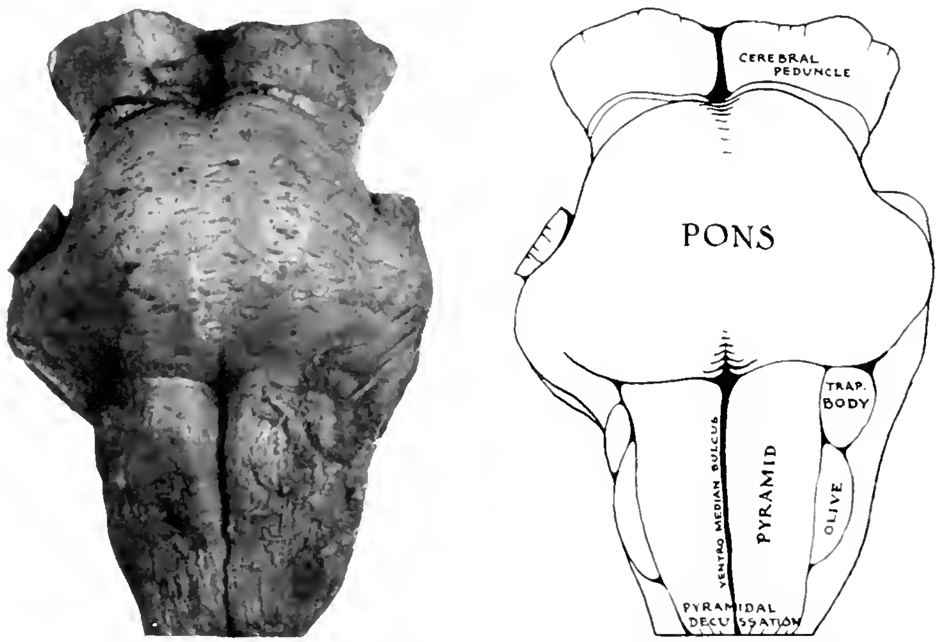


FIG. 205. VENTRAL SURFACE OF BRAIN STEM, GORILLA.
[Actual Length 42 mm.]

KEY TO DIAGRAM. TRAP. BODY, Trapezoid Body.

inferior olivary bodies, by well-defined preolivary sulci. At the caudal extremity of the pyramid, large bundles of interlacing fibers interrupt the ventromesial fissure as the pyramidal decussation carries the fibers of this system from one side to the other across the median line. The interlacing of these crossing pyramidal fibers is more conspicuous than in the lower and intermediate primates. Upon the lateral surface of the oblongata is the tuberculum trigemini which is separated from the inferior olivary body by the deep post-olivary sulcus. The latter, as it extends cephalad, becomes obscured by the dorsal shifting of the dorsal spinocerebellar tract entering the restiform body. At the upper extremity of this body is another elevation upon the lateral surface, the tuberculum acusticum.

The dorsal surface of the oblongata presents the characteristic infra-

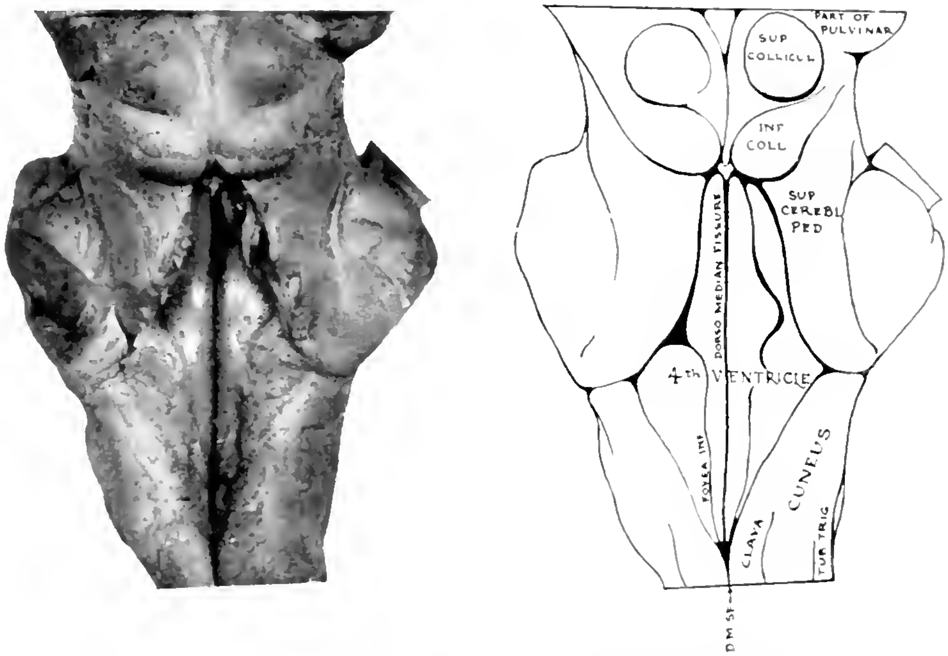


FIG. 206. DORSAL SURFACE OF BRAIN STEM, GORILLA.

[Actual Length 42 mm.]

KEY TO DIAGRAM. D. M. SE., Dorsomedian Septum; FOVEA INF., Fovea Inferior; INF. COLL., Inferior Colliculus; SUP. CEREBL. PED., Superior Cerebellar Peduncle; SUP. COLLICUL., Superior Colliculus; TUB. TRIG., Tuberculum Trigemini.

ventricular and ventricular regions. In the infraventricular region, the dorsomedian septum in the midline separates the two alar plates, each of which is further subdivided by the presence of a dorsal paramedian sulcus. These sulci demarcate the clava which represents the column and nucleus of Goll and the cuneus representing the nucleus and column of Burdach.

In this portion of the oblongata the striking features are the prominence of the pyramid, indicating a probable increase in the volitional control over the somatic musculature; the equally prominent inferior olive, justifying the inference that coordination of simultaneous movements in eyes, head and hands has undergone further extension; and the more clearly marked definition of the dorsal sensory field. This augmentation involves both the column of Goll and the column of Burdach. It more particularly affects the size of the latter, thus denoting accessions to the influx of sensory impulses from the upper extremity and hand. The inferior angle of the ventricular portion of the oblongata is bounded by the diverging clava and cuneus. In this case the cuneus extends a greater distance cephalad than the clava. At the lateral recess the cuneus attains the level of the floor of the ventricle, at which point fibers from the tuberculum acusticum enter the ventricle as the strands of the striae acusticae, while the middle peduncle of the cerebellum forms the sharp cephalic boundary of this recess. The floor of the ventricle near the inferior angle presents the narrow trigonum hypoglossi and, lateral to this, the fovea vagi. There are also indications of an area plumiformis and an area postrema, although neither is so marked as in the average human oblongata. A deep median sulcus divides the floor of the ventricle longitudinally into two symmetrical halves.

In the region of the lateral recess a well-defined prominence makes its appearance. Its relief is not so conspicuous as in the intermediate or even in the lower primates. It marks the position of the vestibular complex. The superior triangle of the fourth ventricle is bounded by the middle cerebellar peduncles and the fibers constituting the superior cerebellar peduncles. Its lateral walls converge toward the caudal orifice of the Sylvian aqueduct and pass beneath the inferior colliculi and the superior medullary velum in the isthmial portion of the stem.

The Pons Varolii. The ventral surface of the oblongata comes to an abrupt termination at the bulbopontile sulcus above which the pons Varolii rises in strong relief as a massive structure crossing the stem. The pons of the gorilla stands next to that of man in prominence. Viewed as an index of the differentiation in the cerebral hemispheres, it signifies an endbrain organization highly advanced in its development.

Other Structures in the Midbrain. A deep basilar groove extends cephalad and gradually widens toward the cephalic margin of the pons Varolii. At this point the divergence in the basis of the midbrain begins, the cerebral peduncles become apparent, and a large optico-peduncular space is disclosed. This space contains the mammillary bodies, the attachment of the infundibular stalk and the tuber cinereum. It is bounded at its cephalic extremity by the optic chiasm and the diverging optic tracts. Upon the dorsal surface of the midbrain appear the usual specializations of the quadrigeminal plates, forming the superior and the inferior colliculi. Of these, the superior colliculi are considerably larger but both sets of elevations have lost in the prominence of their surface relief. The sulci between them, especially the transverse intercollicular sulcus, are less defined than in the intermediate primates, while the cephalic extremity of the longitudinal intercollicular sulcus shows a much wider separation to form the pineal fossa. Upon the lateral surface of the midbrain is a fairly well-outlined mesial geniculate body.

Internal Structure of the Brain Stem in Gorilla

As in all of the primates, the levels upon which these descriptions are based show the critical changes in the brain stem.

LEVEL OF THE PYRAMIDAL DECUSSATION AND THE CAUDAL EXTREMITY OF THE DORSAL NUCLEI (FIGS. 297 AND 298)

At these levels the sections have the characteristic appearance incident to the decussation in the motor pathway with the introduction into the dorsal field of nuclear masses for the relay of sensory stimuli to the higher levels of the neuraxis. The pyramidal system (Py) appears more massive than in any of the primates. The decussation (Pyx) shows the fibers passing from a ventromesial position across the median line to a dorsolateral

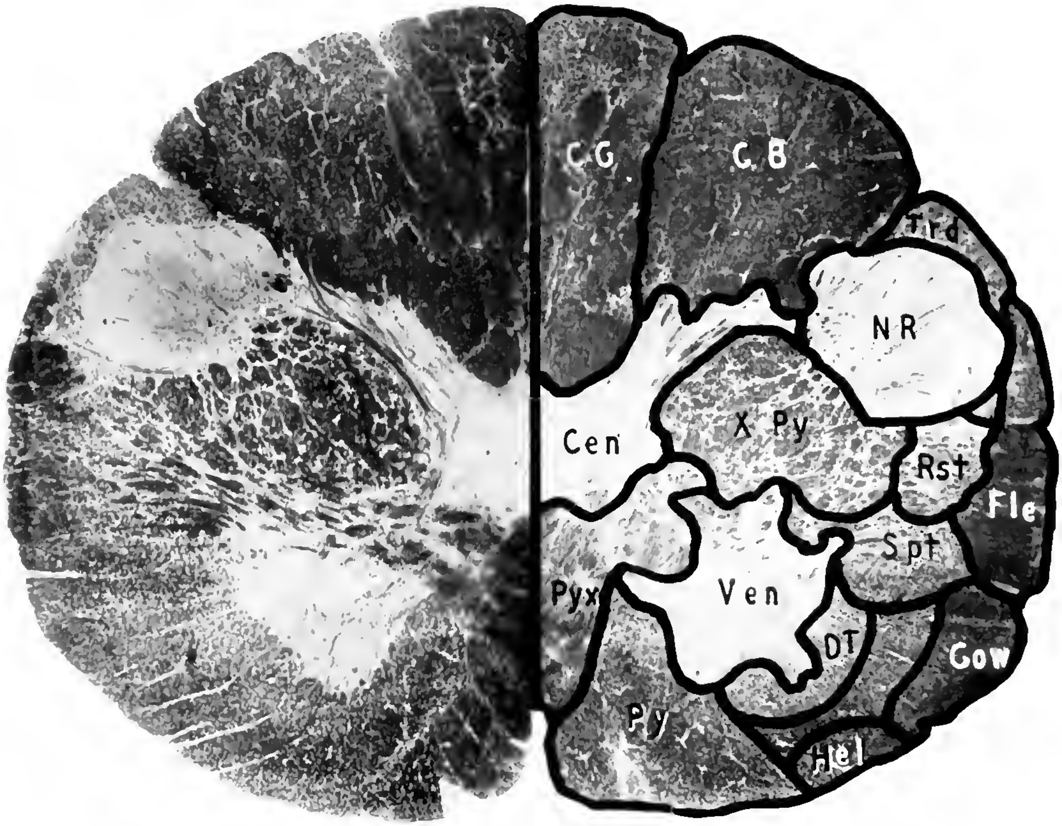


FIG. 207. GORILLA. LEVEL OF THE PYRAMIDAL DECUSSATION.

CB, Column of Burdach; CEN, Central Gray Matter; CG, Column of Goll; DT, Deiterso-spinal Tract; FLE, Dorsal Spinocerebellar Tract; GOW, Ventral Spinocerebellar Tract; HEL, Spino-olivary Tract of Helweg; NR, Nucleus of Rolando; PY, Pyramid; PYX, Pyramidal Decussation; RST, Rubrospinal Tract; SPT, Spino-thalamic Tract; TRD, Descending Trigeminal Tract; VEN, Ventral Gray Column; XPY, Crossed Pyramidal Tract. [Accession J. D. Section 100. Actual Size 13 × 9 mm.]

position on the opposite side. The decussating fibers separate the central gray matter (Cen) from the ventral gray matter (Ven). Passing through the reticular formation are some of the emerging fibers of the eleventh or spinal accessory nerve. Scattered through the dorsal portion of the reticular formation are many bundles of myelinated fibers, the descending portion of the pyramidal tract as it is about to enter the spinal cord (X.Py). The central gray matter by means of a narrow isthmus-like extension is con-

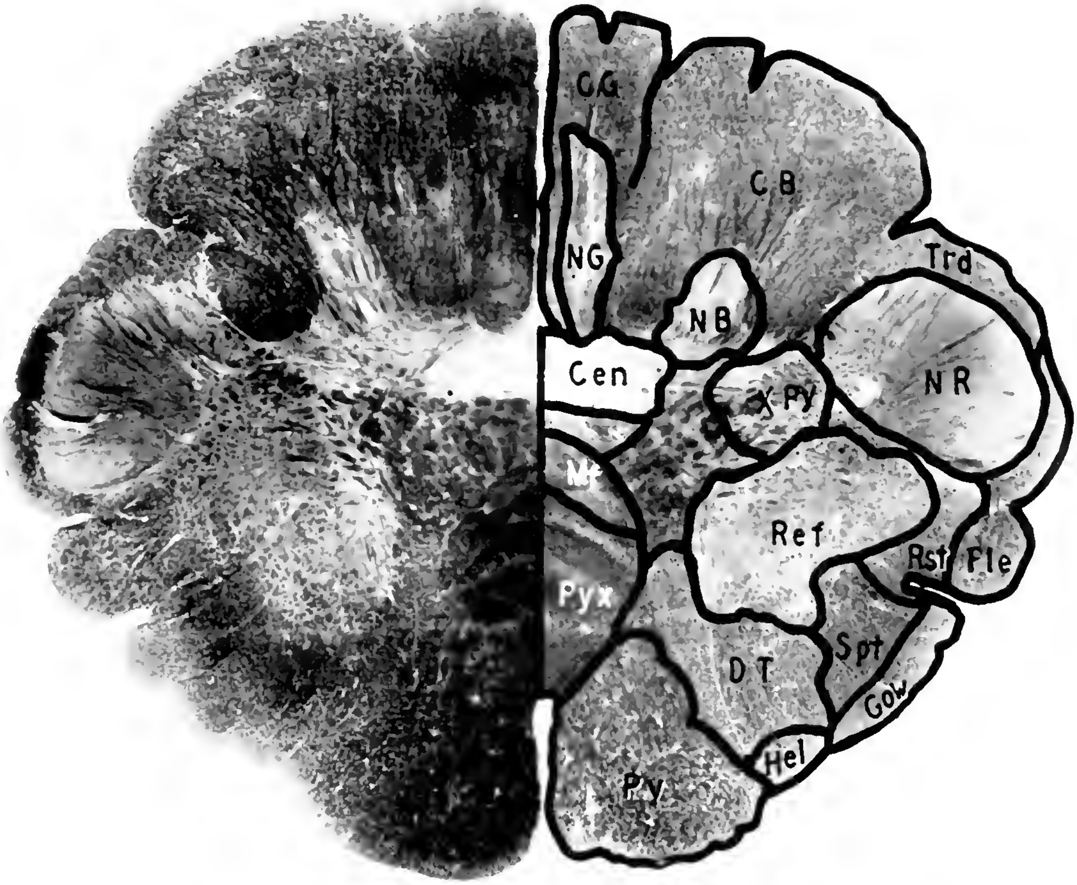


FIG. 298. GORILLA. LEVEL OF THE DORSAL SENSORY NUCLEI.

CB, Column of Burdach; CEN, Central Gray Column; CG, Column of Goll; DI, Deiterso-spinal Tract; DT, Dorsal Spinocerebellar Tract; GOW, Ventral Spinocerebellar Tract; HEL, Spino-olivary Tract of Helweg; ML, Mesial Fillet; NB, Nucleus of Burdach; NG, Nucleus of Goll; NR, Nucleus of Rolando; PY, Pyramid; PYX, Pyramidal Decussation; REF, Reticular Formation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; TRD, Descending Trigeminal Tract; XPY, Crossed Pyramidal Tract. [Accession No. J. D. Section 145. Actual Size 14 × 11 mm.]

nected with three nuclear masses appearing in the dorsal sensory field. The most mesial of these nuclei, and the most faintly developed, is the nucleus of Goll (NG) surrounded by an encapsulating mass of medullated fibers, the column of Goll (CG). Lateral to this is the proximal portion of the nucleus of Burdach (NB) which projects backward into a massive column of Burdach (CB). Occupying the most lateral portion of the dorsal sensory field, and connected by a very narrow strip of gray matter with the central gray, is the substantia gelatinosa trigemini (NR) surrounded on its periphery by the descending trigeminal tract (Trd).

A comparison of these three nuclear elements in the dorsal field, i.e., the nucleus of Goll, the nucleus of Burdach and the nucleus of Rolando (a term applied to the substantia gelatinosa trigemini), gives an accurate idea of the sensory influx from the deep proprioceptive organs of the body. The column of Goll appears to be about one-quarter the size of the column of Burdach, while the trigeminal area is about one-half the size of the latter bundle. In terms of functional capacity it appears from these relations that the influx of sensory impulses from the leg is considerably less than that from the upper extremity and hand; the influx from the head and face occupies an intermediate position between these two. When the great size of the gorilla's fore extremity, the tremendous forearm and highly developed hand, is taken into account compared with that of the leg and foot, the reason underlying the increment in the column of Burdach becomes apparent. On the other hand, the innervation of the head and face does not vary much in its relative dimensions as seen in the intermediate primates. It is, however, considerably less in size than in the lower primates. This fact seems to denote that the cephalic dermatomic areas play a part of less importance in directing the animal's locomotion than they do in such forms as depend largely upon sensory differentiation of the head and face for their guidance.

LEVEL OF THE CAUDAL EXTREMITY OF THE INFERIOR OLIVE (FIG. 299)

Here the lower tip of this structure appears as a circular mass in the ventrolateral region. The circumference of the section shows even more clearly than the external appearance of the brain stem the definition of the sulci which form the boundary lines of the various functional territories in the axis. The ventral paramedian sulcus indicates the lower limit of the pre-

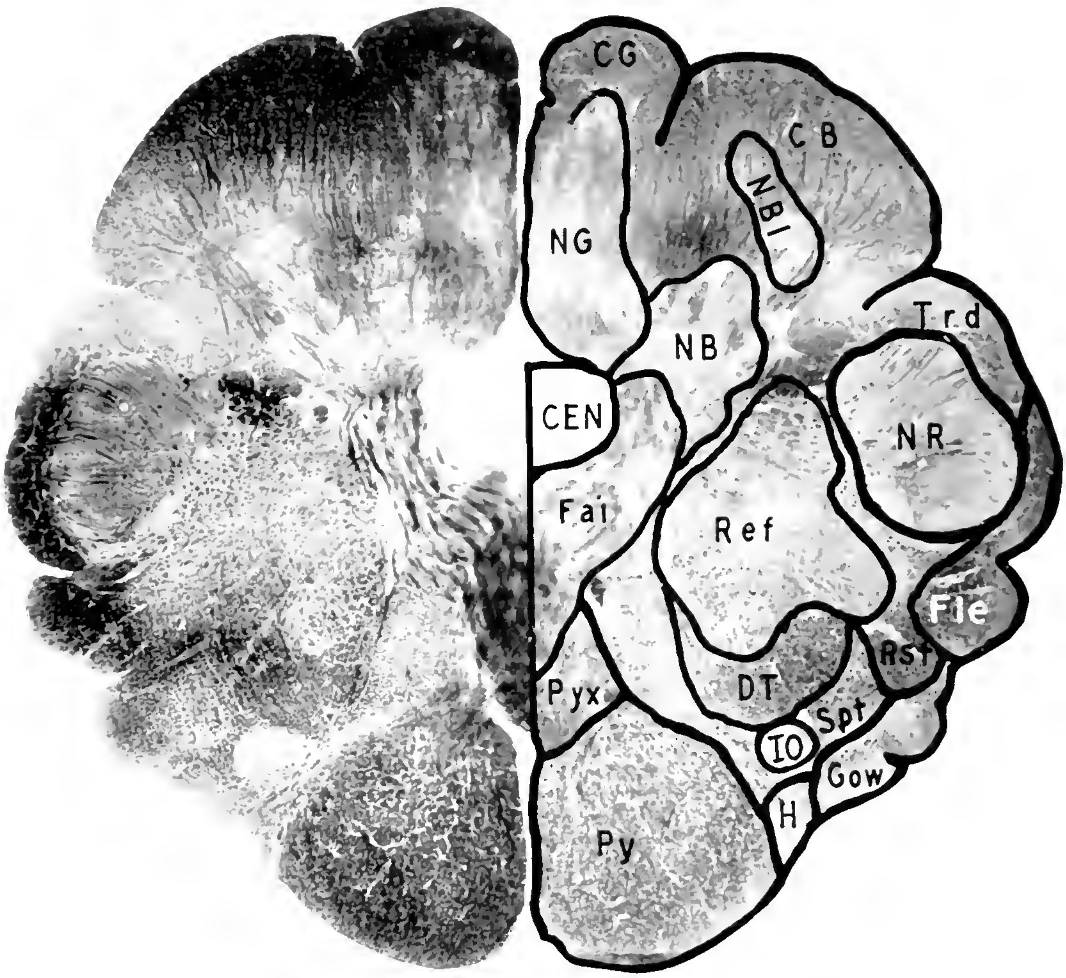


FIG. 209. GORILLA. LEVEL OF CAUDAL EXTREMITY OF INFERIOR OLIVE.

CB, Column of Burdach; CEN, Central Gray Matter; CG, Column of Goll; DT, Deiterso-spinal Tract; FAI, Internal Arcuate Fibers; FLE, Dorsal Spinocerebellar Tract; GOW, Ventral Spinocerebellar Tract; H, Spino-olivary Tract of Helweg; IO, Inferior Olive; NB, Nucleus of Burdach; NBL, Nucleus of Blumenau; NG, Nucleus of Goll; NR, Nucleus of Rolando; PY, Pyramid; PYX, Pyramidal Decussation; REF, Reticular Formation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; TRD, Descending Trigeminal Tract. [Accession No. J. D. Section 195. Actual Size 15 × 13 mm.]

olivary fissure. A small intermediate sulcus in this region demarcates the position of the bundle of fibers constituting the ascending cerebellar tracts, particularly the dorsal spinocerebellar tract (Flc). These delimiting sulci separate corresponding elevations noted on the external surface. The most ventral of these elevations is the pyramid (Py). Lateral to it is the olivary eminence. The first elevation on the dorsal surface is the tuberculum trigemini structurally corresponding to the substantia gelatinosa trigemini (NR). In the dorsal fields are two other eminences, the cuneus (CB) and the clava (CG). Especial attention is called to these elevations and their demarcation upon the surface of the axis as this definition of outline appears increasingly more pronounced in the brain stem of the higher primates. It reaches its most marked prominence in man.

The central gray matter (CEN) appears considerably larger and more quadrilateral in outline than in lower levels. The entire mass has migrated into a more dorsal position preparatory to the opening of the fourth ventricle. Both the nucleus of Goll (NG) and the nucleus of Burdach (NB) have increased in size and afford an opportunity for estimating the relative sizes of the two major nuclei in the dorsal sensory field. The inequality of the two columns of Goll and Burdach is still apparent, thus indicating a greater sensory influx from the arm, forearm and hand than from the lower extremity. The substantia gelatinosa of Rolando (NR) occupies the most lateral position in the dorsal field and is surrounded by the descending trigeminal tract (Trd). The relative size and importance of the pyramidal system may be estimated by the dimensions of the pyramid (Py). Some of the crossing fibers have already assumed their typical descending position in the dorsolateral area. The caudal extremity of the hypoglossal nucleus is seen located in the ventral portion of the central gray matter and arising from it some of its lowermost fibers make their way outward toward the inferior olivary nucleus. The more caudal sections of the brain stem in gorilla afford a basis for estimating the accessions to the voluntary motor control by the proportions of the pyramids. They also disclose the relative sizes and hence the relative functional significance of the three elements entering into the dorsal sensory field, representing collectively the entire influx of sensory impulses pertaining to discriminative sensibility.

LEVEL OF THE MIDDLE OF THE INFERIOR OLIVE (FIG. 300)

At this level certain familiar changes have appeared incident to the alterations in the dorsal field caused by the opening of the fourth ventricle with the gradual conversion of the central gray matter into the floor of this chamber of the brain. Important also is the appearance of the now fully developed inferior olivary body (IO), together with its two major accessory portions, the ventral accessory olive (VO) and the dorsal accessory olive (DO).

The general contour of the cross section is much altered by the appearance of the fourth ventricle. Upon either side of the ventricle, the dorsal paramedian sulcus separates the cephalic extremity of the much attenuated nucleus of Goll (NG) from the large adjacent nucleus of Burdach (NB). The latter nucleus is in turn separated by the dorsolateral sulcus from the tuberculum trigemini whose prominence upon the surface now has been obscured by the dorsal migration of the fibers entering into the restiform body. The post- and preolivary sulci are well defined, separating on the one hand the olivary body from the corpus restiforme, and on the other the pyramid and olive. The central gray matter (Cen) spreads out in a v-shape, forming the lower portion of the floor of the fourth ventricle. In its most mesial portion is the nucleus of the twelfth nerve (Nhy), from which pass the fibers of the hypoglossal nerve. Immediately adjacent to the nucleus of the twelfth nerve in the central gray matter is a collection of gray matter which receives incoming fibers of the pneumogastric nerve; this is the dorsal nucleus of the vagus (Nvd). A much sharper demarcation exists between it and the twelfth nerve nucleus than is the case in the lower primates. Here again, even in these more archaic and fixed structures such as the

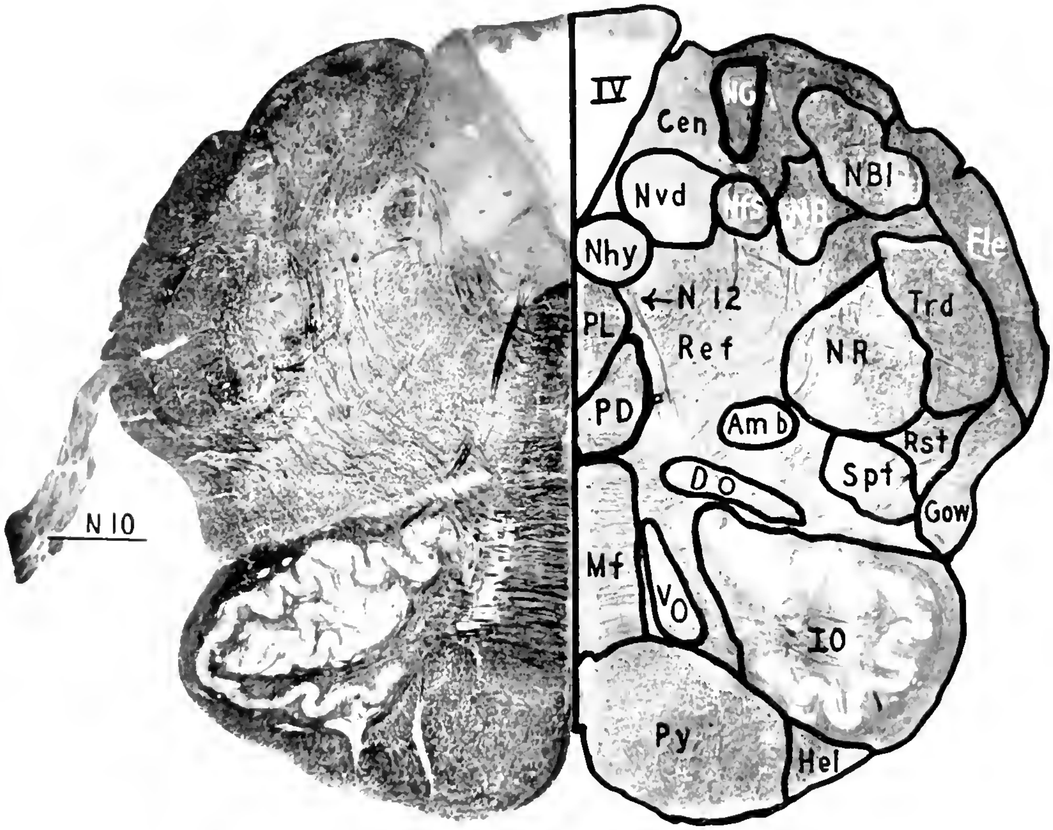


FIG. 300. GORILLA. LEVEL OF THE MIDDLE OF THE INFERIOR OLIVE.

AMB, Nucleus Ambiguus; CEN, Central Gray Matter; DO, Dorsal Accessory Olive; FLE, Dorsal Spinocerebellar Tract; GOW, Ventral Spinocerebellar Tract; HEL, Spino-olivary Tract of Helweg; IO, Inferior Olive; MF, Mesial Fillet; NB, Nucleus of Burdach; NBL, Nucleus of Blumenau; NFS, Fasciculus Solitarius; NG, Nucleus of Goll; NHY, Hypoglossal Nucleus; NR, Nucleus of Rolando; NVD, Dorsal Vagal Nucleus; N10, Tenth Cranial Nerve; N12, Twelfth Cranial Nerve; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PY, Pyramid; REF, Reticular Formation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; TRD, Descending Trigeminal Tract; VO, Ventral Accessory Olive; IV, Fourth Ventricle. [Accession No. J. D. Section 330. Actual Size 18 × 11 mm.]

cranial nerve nuclei, there is a greater degree of definition in the advanced species of the primate order. This increasing definition of all the structures of the brain stem is a characteristic of progressive differentiation and is especially well emphasized in the higher primates.

In the lateral wall of the ventricle is a nuclear mass, the most mesial portion of which represents the attenuated upper extremity of the nucleus of Goll (NG). Arcuate fibers pass from it forward and inward toward the median raphe to enter the mesial fillet (Mf). The adjacent nucleus of Burdach (NB), as already indicated, is separated by a faintly discerned dorsal paramedian sulcus, and presents itself as a more or less scattered aggregation of nuclear substance. The outer portion of the nucleus of Burdach is the nucleus of Blumenau (NBl). In the gorilla it is especially complex in arrangement and large in size. Occupying a position ventral to the nucleus of Burdach is the substantia gelatinosa trigemini (NR) now somewhat obscured by the crowding fibers which form the restiform body.

In the lateral extremity of the central gray matter (Cen) is a dense bundle of fibers, somewhat oval in outline, the fasciculus solitarius (Nfs), coming into relation with which are the entering fibers of the vagus nerve. The reticular formation occupies the central portion of the section (Ref). It is crossed by many internal arcuate fibers taking origin in the nucleus of Burdach and following a course which leads to the raphe and the decussation of the mesial fillet (Mf). Occupying the most ventromesial portion of the section are the fibers of the pyramidal system forming the pyramid (Py). The inferior olive (IO), showing not only an increment in volume but added complexity in its convolutions, indicates to what extent there has been an increase in the control of simultaneous movements of head, eyes and hand, and in the facilitation of coordination of all skilled learned performances. This observation supports the idea that the gorilla has made definite advances toward that ultimate goal in which the hands are eventually freed from direct participation in locomotion. Such manual emancipation provides a means for exploring the environment more extensively, for creating new modes of action, for augmenting the stream of sensory impressions from contacts heretofore unknown—in a word, for the discovery and control of new territories in the realm of behavior. How much more the hand actually means to the gorilla than to any of the lower primates may be inferred from the history of John Daniel who, in many particulars, approached the human standards of manual manipulation. In the acquisition of these manipulations, as well as in their execution, a harmonious interaction is necessary between the muscles of the eyeballs, of the neck moving the head in the various directions, of the forearms, arms and hands in order that the object of these movements may be attained. The structural expansion of the inferior olivary nucleus accords closely with the increment in function witnessed in the increased capacity of the gorilla for the simultaneous regulation of eyes, head and hand. The evolutional unfolding of the inferior olivary body is one of the most striking features in the brain stem of the primates.

The features of the brain stem selected for comparative study of their evolutional relations in the primate order were those which appeared to be most susceptible to the influences of progressive adaptation. Such influences of evolutional progress do not, however, confine themselves to these more plastic structures. They also affect certain archaic elements which represent the essential foundations of neural organization upon which the vital processes of life depend. Structures, for example, like the nuclei of the cranial nerves which regulate the action of the heart, the rate and rhythm of respiration, the peristaltic movements of the gastrointestinal canal, the reflex movements of the tongue, lips, nose, soft palate and larynx in acts of swallowing, breathing and emission of vocal sounds come into this category. All of them represent the biological framework essential to the actual process of living. They might for this reason be considered to possess an inflexibility both in design and arrangement because of the unchanging nature of the functions over which they preside. Yet even such archaic, fixed structures in the brain stem show a degree of modification which is worthy of note as emphasizing the fact that they, for all their primitiveness, have felt and responded to the influences of progress. Thus, in passing from the lowest to the highest members of the group, these archaic structures, the cranial nerve nuclei, show a steadily increasing definition in their outline as they assume more distinctive individuality and greater dimensions in each successive grade of differentiation in the primates.

LEVEL OF THE VESTIBULAR AND CEREBELLAR NUCLEI (FIGS. 301–304)

Here the striking feature is the replacement of the nuclei of Goll and Burdach by a large vestibular complex composed of the nucleus of Deiters (ND) and the triangular nucleus of Schwalbe (NSe). These two nuclear masses have gained in definition but are considerably less prominent from the dimensional standpoint than in some of the lower primates, especially those whose life is preeminently arboreal. The central gray matter (Cen) occupies a position under the subependymal gray in the floor of the fourth ventricle (Fig. 301). It contains in its most lateral portion the nucleus of Schwalbe (NSe). Lateral to this is a large-celled nuclear aggregation, the nucleus of Deiters (ND). Ventral to Deiters' nucleus is the somewhat reduced substantia gelatinosa trigemini (NR) on whose outer margin descends the trigeminal tract (Trd). In a position lateral to Deiters' nucleus lies the massive collection of fibers constituting the restiform body (ICP) about to form the inferior cerebellar peduncle and thus consummate the connection between the cerebellum, the spinal cord and the oblongata. In their usual ventromesial position are the collected bundles constituting the pyramid (Py), and dorsal to it the fasciculus of the mesial fillet (Mf). The cephalic extremity of the inferior olive occupies a position lateral to the pyramid and still shows its complex convoluted outline (IO).

From the functional standpoint, this section in gorilla takes its signifi-

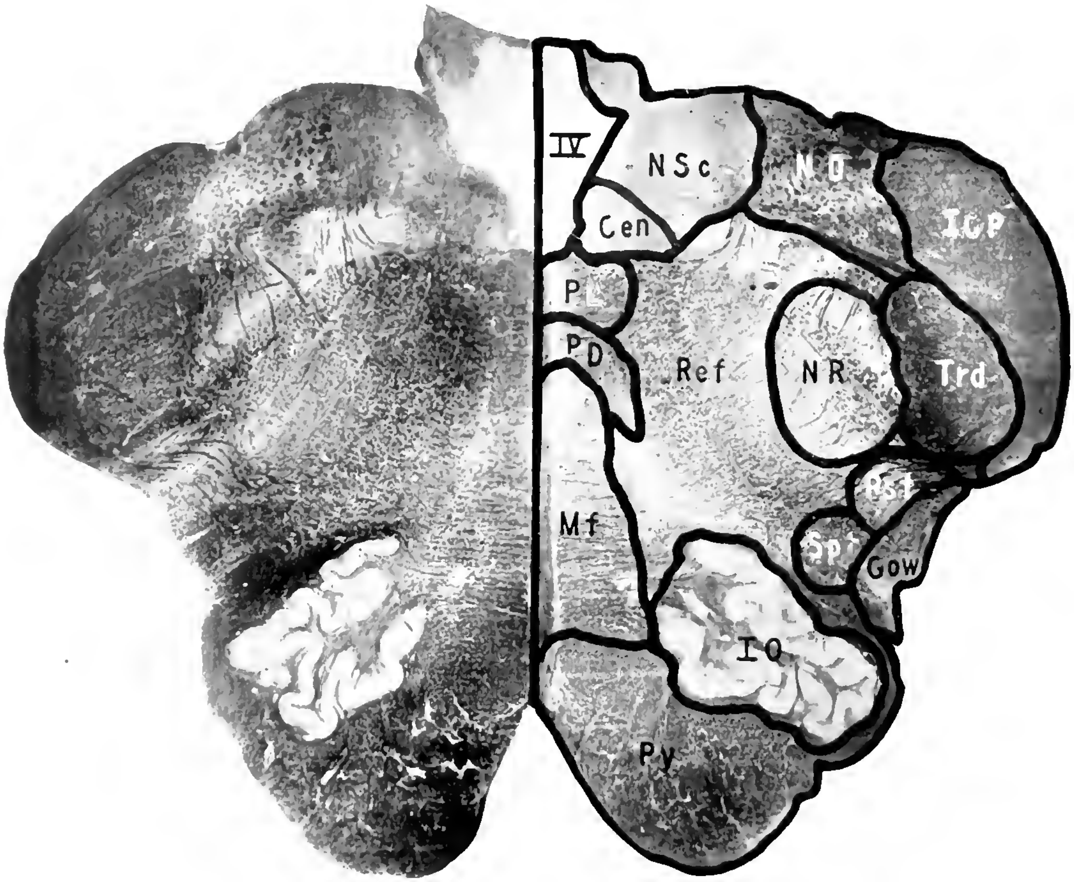


FIG. 301. GORILLA. LEVEL OF THE VESTIBULAR NUCLEI.

CEN, Central Gray Matter; GOW, Ventral Spinocerebellar Tract; ICP, Inferior Cerebellar Peduncle; IO, Inferior Olive; MF, Mesial Fillet; ND, Nucleus of Deiters; NR, Nucleus of Rolando; NSC, Nucleus of Schwalbe; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PY, Pyramid; REF, Reticular Formation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; TRD, Descending Trigeminal Tract; IV, Fourth Ventricle. [Accession No. J. D. Section 376. Actual Size 20 × 13 mm.]

cance from the fact that the central balancing mechanism appears to be less highly specialized than in many of the lower forms. This apparent difference calls for some explanation in the behavior of the animal. It may well be that the gorilla which, because of its great weight, has ceased to live so much in the trees, and especially in the uppermost portions of them where the branches are too small to bear it, has in consequence changed its modus

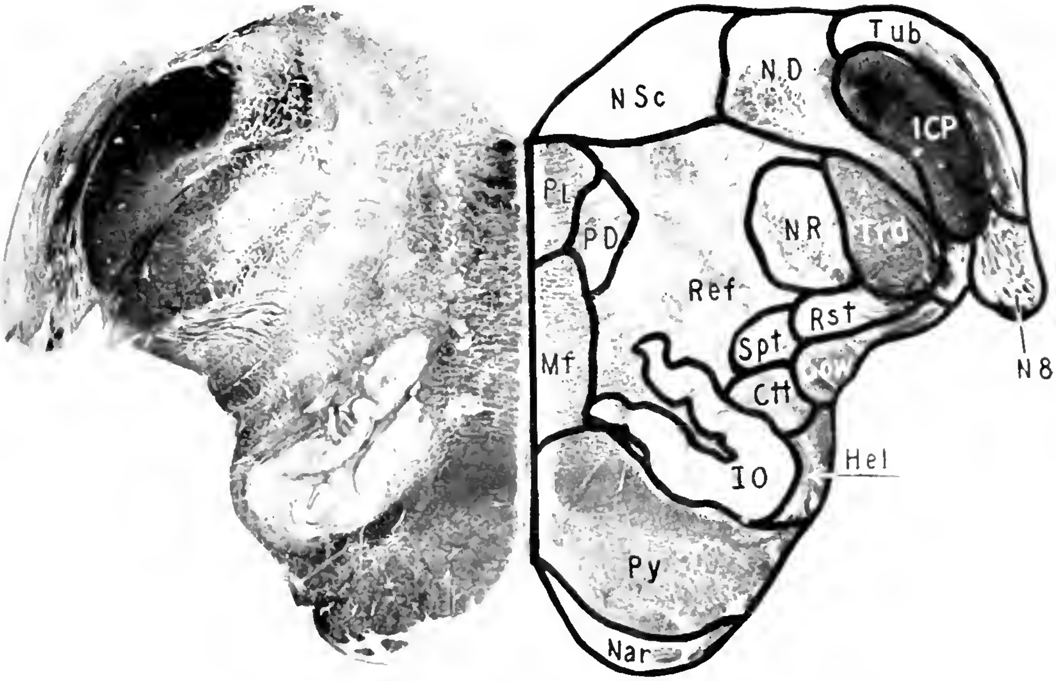


FIG. 302. GORILLA. LEVEL OF THE VESTIBULAR NUCLEI.

CTT, Central Tegmental Tract; GOW, Ventral Spinocerebellar Tract; HEL, Spino-olivary Tract of Helweg; ICP, Inferior Cerebellar Peduncle; IO, Inferior Olive; MF, Mesial Fillet; NAR, Nucleus Arciformis; ND, Nucleus of Deiters; NSC, Nucleus of Schwalbe; NR, Nucleus of Rolando; N8, Auditory Nerve; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PY, Pyramid; REF, Reticular Formation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; TRD, Descending Trigeminal Tract; TUB, Tuberculum Acusticum. [Accession No. J. D. Section 401. Actual Size 22 × 9 mm.]

vivendi to a terrestrio-arboreal adaptation. On the other hand, this recourse to ground-living does not require so much in the way of balancing function as in those animals which depend wholly upon the arboreal highways for their existence. Indeed, the almost quadrupedal locomotion of gorilla would not in itself call for a highly developed balancing mechanism. Even if the gorilla does stand upright upon its hind legs at times, it is only poorly adjusted to this posture. As a matter of fact, this position is so infrequently assumed and performed in such ungainly manner as to require in and of itself but small functional representation in the central axis.

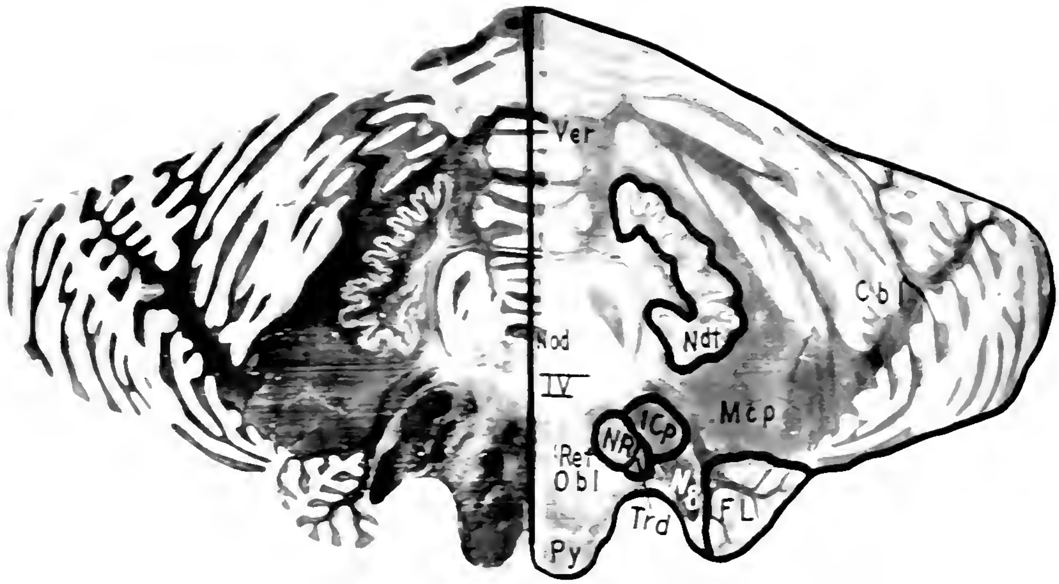


FIG. 303. GORILLA. LEVEL OF THE CEREBELLAR NUCLEI.

CBL, Cerebellum; FL, Flocculus; ICP, Inferior Cerebellar Peduncle; MCP, Middle Cerebellar Peduncle; NDT, Dentate Nucleus; NOD, Nodulus; NR, Nucleus of Roller; N8, Auditory Nerve; OBL, Oblongata; PY, Pyramid; RET, Reticular Formation; TRD, Descending Trigeminal Tract; VER, Vermis; IV, Fourth Ventricle. (Accession No. J. D. Section 5?5. Actual Size 25 × 25 mm.)

The cerebellar nuclei and particularly the dentate nucleus (Ndt) show a most striking advance (Fig. 303). Not only has there been a great increase in the size of this nucleus which represents the efferent transmission of cerebellar impulses, but it has also manifested that outstanding feature of specialization whenever cerebral expansion is necessary, namely, a greater tendency toward convolution. The nucleus dentatus in gorilla is much more highly organized in this particular than in either the orang-outang or chimpanzee. This differentiation furnishes another reason for the claim that in certain details of its encephalic structure the gorilla stands nearer to man than the other two great anthropoids. The functional significance of the expansion, increased definition and convolution of the dentate nucleus of gorilla, as compared with the lower members of the primate group, needs

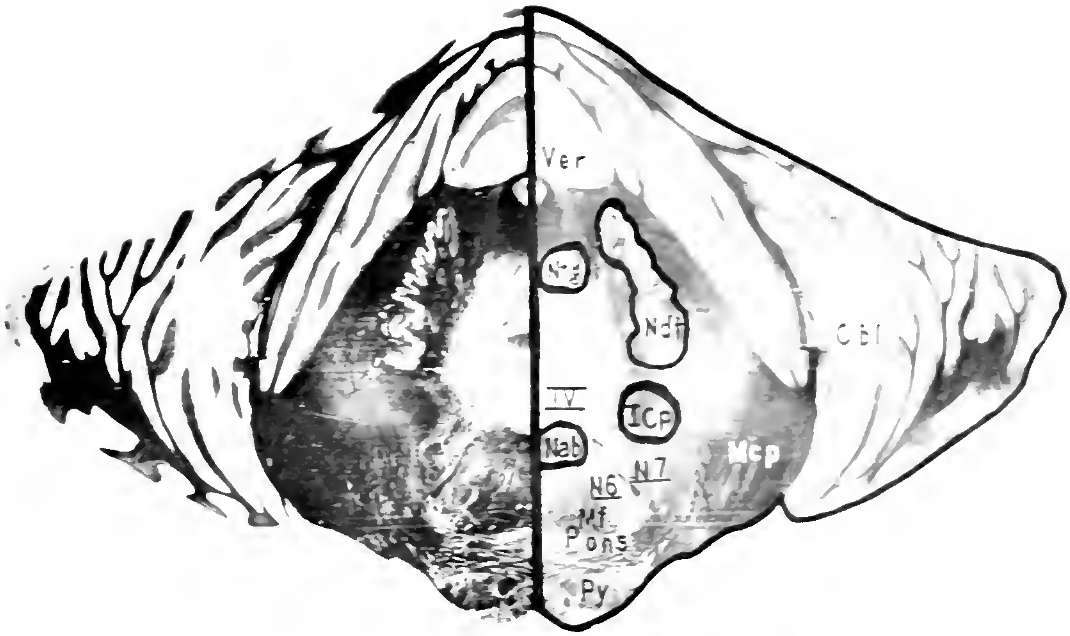


FIG. 304. GORILLA. LEVEL OF THE CEREBELLAR NUCLEI.

CBL, Cerebellum; ICP, Inferior Cerebellar Peduncle; [illegible] NAB, Abducens Nucleus; NDT, Dentate Nucleus; [illegible] Nerve; PY, Pyramid; VER, Vermis; [illegible] 22 mm.)

scarcely more than passing mention. This point has been touched upon so frequently with reference to cerebellar organization, that its bearing must be clear. In gorilla the cerebellum shows notable expansions in the region of its lateral lobes (Cbl), which have their efferent representation in the dentate nuclei. The vermis (Ver), in which is vested coordinating mechanism for control of the axial and paraxial musculature of the body, has manifested no such progressive advance. It has in fact shown but little variation throughout the entire vertebrate phylum because the axial musculature is rigidly fixed in [illegible] For this reason it has displayed less tendency [illegible] whereas the muscles in the extremities represented in the progressively expanding lateral lobes of the cerebellum have [illegible] functional adaptation.

LEVEL OF EMERGENCE OF SIXTH CRANIAL NERVE, NERVUS ABDUCENS (FIG. [illegible])

At this level the first pontile elements make their appearance with the [illegible]. The elements of the pons constitute [illegible] masses [illegible] occupying a basal position. These are the [illegible] (PN). Other elements of the pons [illegible] at this level are [illegible] cerebellar system. The central gray matter [illegible] forms [illegible] of the fourth ventricle and in its [illegible] a large nucleus (N[illegible]) which gives rise to the sixth cranial nerve [illegible] (N[illegible]). The fibers of this [illegible]. They appear among the [illegible] pyramidal system (P[illegible]). The more medial [illegible] (PN) represents the continuation cephal[illegible] the nucleus [illegible] second portion in the emergent [illegible] (N[illegible]). The first portion of the emergent [illegible] in their typical spray-like form [illegible]. The [illegible] portion of the emergent [illegible] toward its point [illegible] pontile sulcus. The [illegible] of the seventh nerve pass [illegible] substantia gelatinosa trigemini (NR[illegible]) [illegible] densely compacted [illegible] the descending tract of the trigeminal [illegible].

The reticular formation constitutes the major portion of the tegmentum and is separated from the basis by the medial [illegible] (M[illegible]). Penetrating the collected bundles of the medial [illegible] are a number of trans-

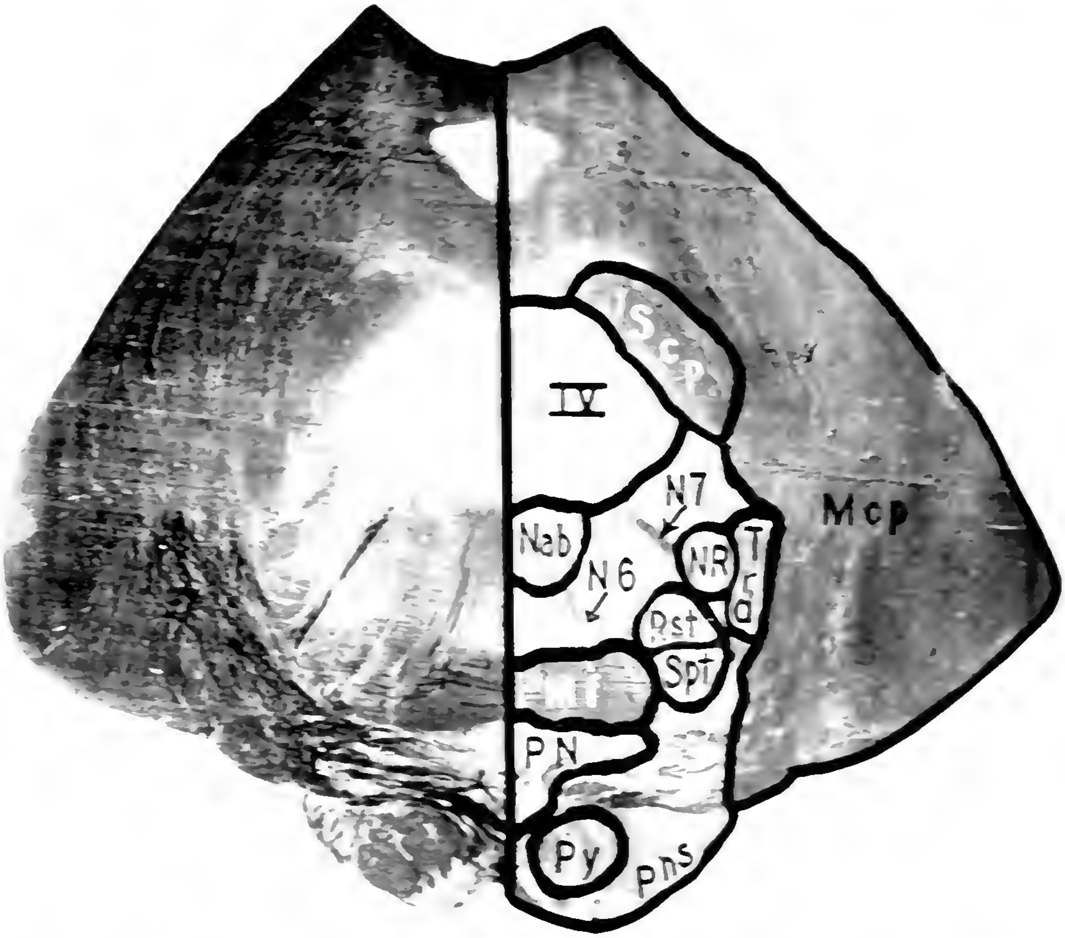


FIG. 30 A. [illegible]

verse fibers in process of decussation. These fibers belong to the secondary cochlear pathways and constitute the [illegible] [illegible] ascending axons subsequently form the lateral (auditory) fillet. The outstanding feature of this level is the size of the pontile nuclei. These nuclei in gorilla, as in all of the great anthropoids and man, are so exuberant in their development as to require an extension beyond the pontile segments of the axis which usually suffice to contain them. Their caudal continuation projects into the ventral surface of the pyramid in the oblongata. The extension of the pontile nuclei beyond the actual metencephalic limits denotes an increment in the functions of the pons which appears striking when the gorilla is compared with the lower forms.

The heavy masses of medullated fibers flanking the ventricular walls are composed of axons of the middle and superior cerebellar peduncles (Mcp, Scp). They furnish a good index as to the richness of connection between the cerebellum and other segments of the central nervous system.

LEVEL THROUGH THE MIDDLE OF THE PONS VAROLII (FIG. 306)

Here the contour of the cross section has been materially altered by the central addition of the massive structures forming the pons Varolii. The three characteristic pontile layers differ from those encountered in the lower and intermediate primates in the greater complexity of their several strata. There is a marked increased depth in the stratum superficiale, while in the stratum complexum there are more fibers and a greater nuclear mass constituting the pontile nuclei (PN). The stratum profundum is also of greater depth. The fibers of all three strata become confluent to form a more extensive middle cerebellar peduncle (Mcp). Scattered in the midst of the stratum complexum are the fibers of the pyramidal system (Py) which, however, appear in much more disseminated arrangement because of the greater complexity of the nuclear mass, and the decussating pallio-ponto-cerebellar fibers. The central gray matter (Cen) now surrounds the much reduced approach to the Sylvian aqueduct. It contains in its lateral extremity the mesencephalic root of the trigeminal nerve. The lateral walls are formed by a dense mass of fibers constituting the superior cerebellar peduncle (Sc p), lateral to which is the tractus uncinatus

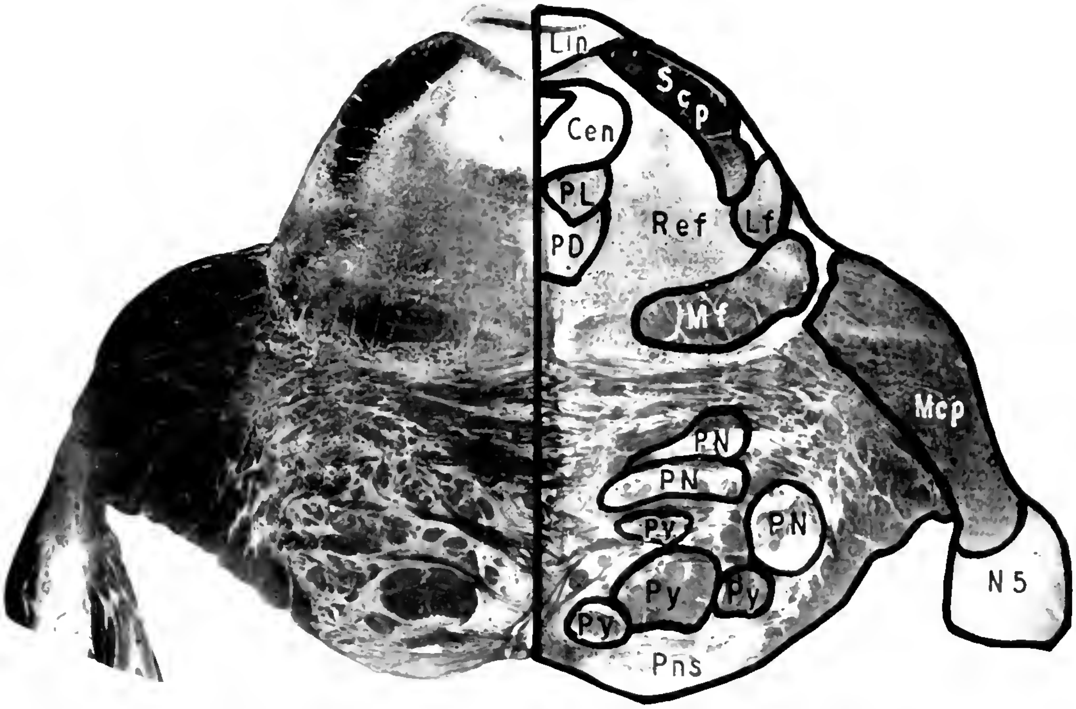


FIG. 306. GORILLA. LEVEL THROUGH THE MIDDLE OF THE PONS VAROLII. CEN, Central Gray Matter; LL, Lateral Fillet; LIN, Lingula; MCP, Middle Cerebellar Peduncle; MF, Mesial Fillet; N5, Trigeminal Nerve; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PN, Pontile Nuclei; PNS, Pons; PY, Pyramid; RET, Reticular Formation; SCP, Superior Cerebellar Peduncle. [Accession No. J. D. Section 580. Actual Size 30 × 10 mm.]

of Russel, and overlying this is a thin stratum of fibers, the ventral spino-cerebellar tract, making its way toward the vermis of the cerebellum.

In the lateral portion of the pons Varolii, as its axons become collected to form the middle cerebellar peduncle, fibers from the dorsal root of the trigeminal nerve (N 5) penetrate the pons. These fibers make their way into the tegmentum where they terminate in relation with the cephalic extremity of the substantia gelatinosa trigemini. The tegmentum pontis has as its boundary the transversely disposed fibers of the mesial fillet (Mf), at whose lateral extremity is the bundle of fibers forming the lateral fillet (Lf). In functional significance, this level takes its importance from the size and character of the pons Varolii as well as the dimensions of the superior cerebellar peduncle, both indicating the degree to which the cerebellum has expanded. It denotes accessions in the development of coordinative control over the animal's acquired, skilled movements. The impression conveyed by the pontile nuclei and pallio-pontile system of fibers in gorilla is that this animal is possessed of a wider range of behavioral reactions than is the case in the lower or intermediate primates.

LEVEL OF THE EMERGENCE OF THE TROCHLEAR NERVE (FIG. 307)

Here the section is beginning to assume the character of transition from the pons Varolii to the midbrain. The central gray matter (Cen) entirely surrounds the beginning of the aqueduct of Sylvius in whose roof the fibers of the fourth nerve (nervus trochlearis) (N4) make their emergence from the stem. The tegmental portion of the axis at this level is separated from the basis by the characteristic boundary line, the transversely disposed bundle of the mesial fillet (Mf). The basal portion of the section still has the typical appearance of the pons Varolii, showing the three characteristic layers, the stratum superficiale, the stratum complexum and the stratum profundum. The ventromedian furrow along the surface of the pons is now becoming deeper, preparatory to the final separation of the two halves of the basis which, in the midbrain levels, gives rise to the divergence eventuating in the formation of the two cerebral peduncles.

LEVEL OF THE INFERIOR COLLICULUS (FIG. 308)

At this level the configuration of the section is changed by the appearance of two dorsal elevations above the roofplate of the aqueduct of Sylvius.

These are the inferior colliculi (IC). Both in size and in complexity of their stratification, the colliculi in the gorilla show some reduction as compared with the lower and intermediate primates. This fact is consonant with

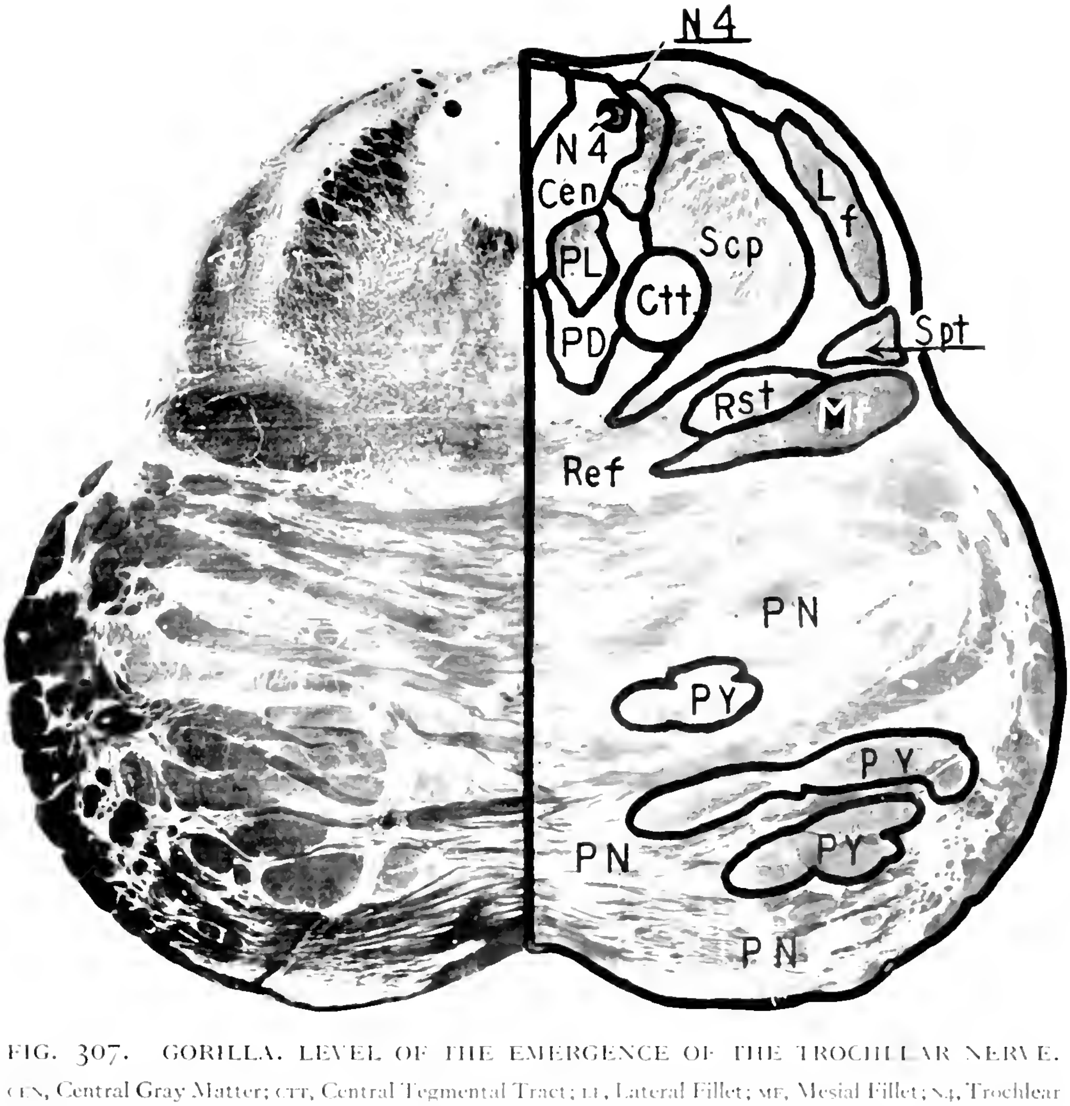


FIG. 307. GORILLA. LEVEL OF THE EMERGENCE OF THE TROCHLEAR NERVE.

CEN, Central Gray Matter; CTT, Central Tegmental Tract; LF, Lateral Fillet; MF, Mesial Fillet; N4, Trochlear Nerve; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PN, Pontile Nuclei; PY, Pyramid; REF, Reticular Formation; RST, Rubrospinal Tract; SCP, Superior Cerebellar Peduncle; SPT, Spinothalamic Tract. [Accession No. J. D. Section 754. Actual Size 23 × 20 mm.]

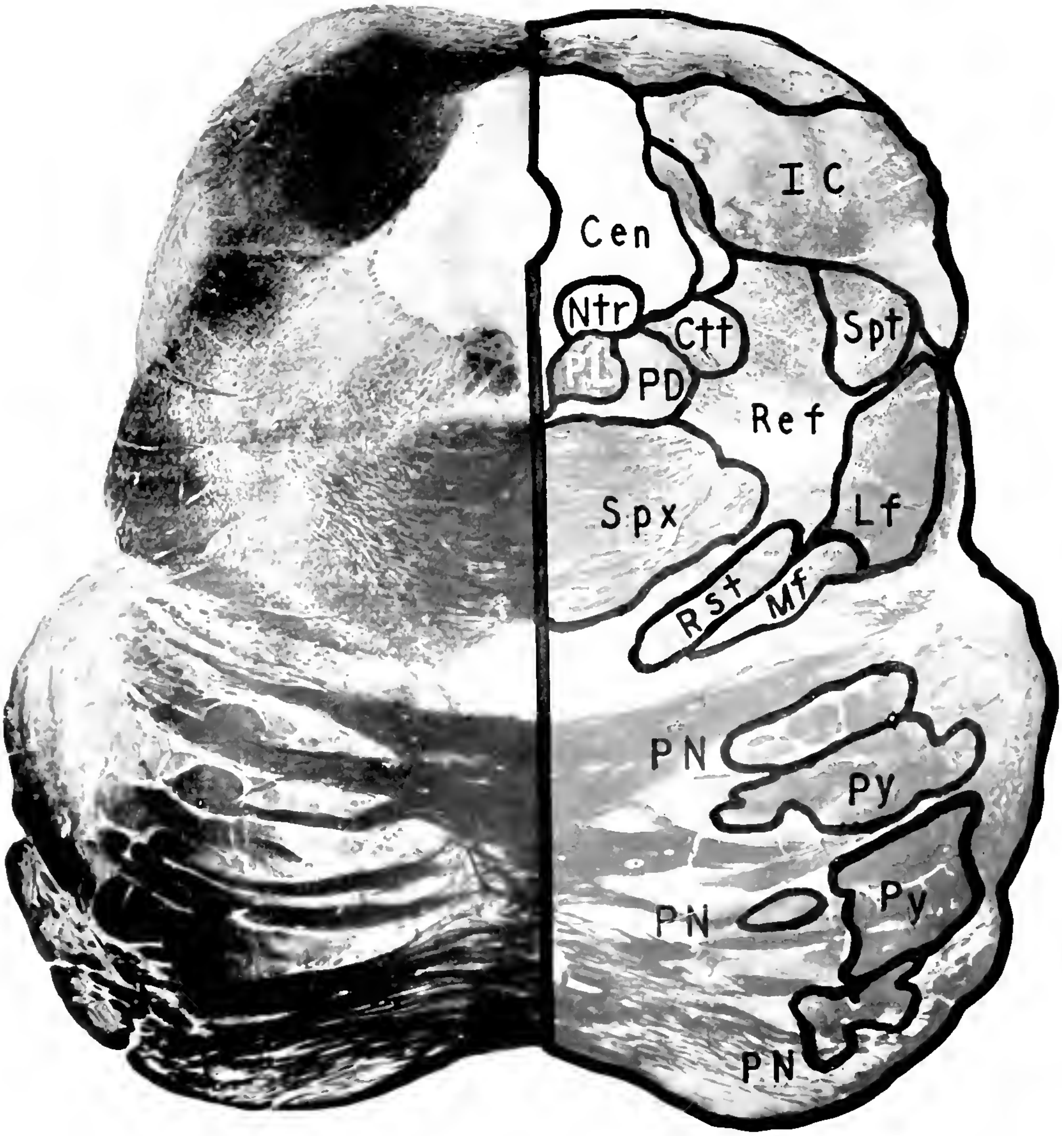


FIG. 308. GORILLA. LEVEL OF THE INFERIOR COLLICULUS.

CEN, Central Gray Matter; CTT, Central Tegmental Tract; IC, Inferior Colliculus; LF, Lateral Fillet; MF, Mesial Fillet; NTR, Trochlear Nucleus; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PN, Pontile Nuclei; PY, Pyramid; REF, Reticular Formation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; SPX, Crossing of Superior Cerebellar Peduncle. [Accession No. J. D. Section 815. Actual Size 22 × 22 mm.]

the increased expansion in the temporal region especially in the auditory area of the hemisphere. Thus, in gorilla, as also in the other higher anthropoids, the function of hearing has undergone a marked degree of telencephalization. The temporal lobe is not only larger, but also more complexly convoluted. The central gray matter (Cen) surrounds the much reduced ventricular space forming the Sylvian aqueduct. In the roofplate above the aqueduct are seen decussating fibers of the inferior collicular commissure. In the ventral portion of the central gray matter near the midline is a well-defined aggregation of nerve cells constituting the nucleus trochlearis (Ntr) from which emergent fibers of the fourth nerve take origin. On the lateral boundary of the central gray matter is a thin zone of heavily myelinized axons, the tractus mesencephalici trigemini. Lateral to this tract is the extensive mass constituting the inferior colliculus which appears to retain some of its primitive stratified arrangement. The stratum superficiale griseum is clearly defined, but because of its deficiency in histological detail, has a definitely vestigeal appearance. Four other layers may be discerned. The primordial tendency of this portion of the brain to present definite stratification is still retained even in this high representative of the primate order.

The boundary between the tegmentum and basis in this portion of the axis is, as in preceding sections, determined by the mesial fillet (Mf). The tegmentum itself contains a large and somewhat diffuse reticular formation (Ref) in the center of which, in process of complete decussation, are the fibers of the superior cerebellar peduncle (Spx). The basis has many of the appearances typical of the pons Varolii. The scattered bundles of the pyramidal system (Py) are showing a tendency to reassemble as a single fasciculus. The basilar groove along the ventral surface of the pons has become deeper as it approaches the point of divergence of the cerebral peduncles.

LEVEL OF THE SUPERIOR COLLICULUS (FIG. 309)

Here the general contour of the section has undergone marked alteration primarily due to the divergence of the cerebral peduncles (CP).

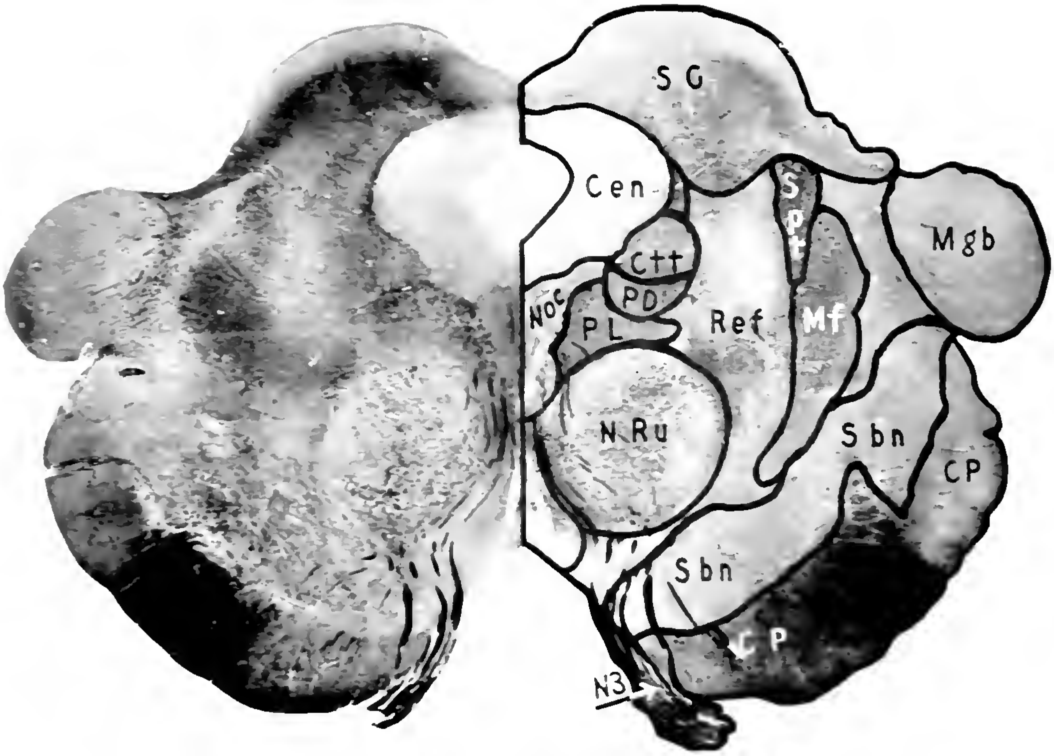


FIG. 309. GORILLA. LEVEL OF THE SUPERIOR COLLICULUS.

CEN, Central Gray Matter; CP, Cerebral Peduncle; CTT, Central Tegmental Tract; MF, Mesial Fillet; MGB, Mesial Geniculate Body; NOC, Nucleus Oculomotorius; NRU, Nucleus Ruber; N3, Oculomotor Nerve; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; RET, Reticular Formation; SBN, Substantia Nigra; SC, Superior Colliculus; SPT, Spino-thalamic Tract. Accession No. J. D. Section 555. Actual Size 30 × 15 mm.]

In the dorsal region are the two fairly prominent elevations forming the superior colliculi (SC). The section is further characterized by the appearance near the center, in the reticular formation, of a large specialized nuclear mass, the nucleus ruber (NRu). The superior colliculi contain indications of being the vestige of the once conspicuous optic lobes in the lower vertebrates. Their reduction is clearly shown in gorilla by a demonstrable decrease in size and by the vestigeal condition of their stratification. A few layers of cells and fibers, rather indiscriminately arranged, may still be observed upon high magnification. The central gray matter (Cen) surrounds the aqueduct of Sylvius, and in its ventromesial portion contains one of the largest of the cranial nuclei, the nucleus oculomotorius (N.oc.). This nucleus is important not only because of the extremely delicate musculature which it controls, but quite as much because of the close internuclear relation which is maintained between the two nuclei by means of decussating and commissural fibers. No other structures in the body are more dependent upon mutual cooperation than the eyeballs. The slightest deflection in their adjustment produces gross defects in visual perception which may not only disorganize the appreciation of objects, but also disturb many of the reactions of the animal in relation to its external accommodations. It is the prominence of these internuclear commissural and decussating fibers which makes the nucleus oculomotorius in gorilla particularly conspicuous.

The emergent fibers of the oculomotor nerve pass forward, some of them penetrating the inner margin of the red nucleus (N.R.), some of them skirting its margin, to reach the sulcus oculomotorius in the optic-peduncular space. The nucleus ruber (N.R.) is a large and highly differentiated structure in the tegmentum, acting as a relay station for the efferent course of impulses from the cerebellum. The marked increment in this nucleus, combined with the increased definition in the size of the dentate nucleus and the expansion of the superior cerebellar peduncle, indicates that large functional accessions have been made in coordinative control of the animal's muscular system. Such additional coordination in the muscular activity of the gorilla is primarily determined by the development of greater manipulability of the upper extremities and especially of the hands. The feet and legs have shown relatively less increase in specialization for the primates. Because of the advanced differentiation in the nucleus ruber, the reticular formation (Ref) seems to be a less diffuse and more definitely circumscribed structure. This tendency for the archaic constituents of the brain to gain an increasingly more precise definition is a feature which distinguishes gorilla in its evolutionary progress toward the standards attained by the highest development of the nervous system.

The dense reticular formation passes laterally without a sharp line of demarcation into the protuberance forming the mesial geniculate body (Mgb). It appears to become more sharply defined in a ventral direction as a discrete nuclear mass extending from the midline to the extreme periphery of the section. This is the substantia nigra (Sbn) whose function in connection with certain automatic associated movements has already been suggested, although much doubt still exists with regard to its exact physiological significance. Ventral to the substantia nigra is a very dense mass of fibers constituting the cerebral peduncle (CP) which contains the collected nerve fibers of the pyramidal system as well as all those axons constituting the pallio-ponto-cerebellar system. Thus the cerebral peduncle offers an opportunity to estimate at a glance the size and proportion of those systems of fibers which convey the two great concurrent streams necessary to all skilled motor performances: first, the palliospinal or pyramidal system which serves for the transmission of impulses necessary for the voluntary control of the movement, and second, the pallio-ponto-cerebellar system, for the transmission of impulses which call into play the simultaneous cooperation of the coordinative regulation by the cerebellum.

In the more lateral portion of the reticular formation is an irregular collection of fibers constituting the mesial fillet (Mf) which has here departed somewhat from the position occupied by it throughout the pons Varolii. This deflection of its course is preparatory to its entrance into the optic thalamus.

LEVEL OF THE OPTIC CHIASM (FIG. 310)

At this level a marked change in the outline of the section is determined by the appearance of the third ventricle (V 3) and the two optic thalami.

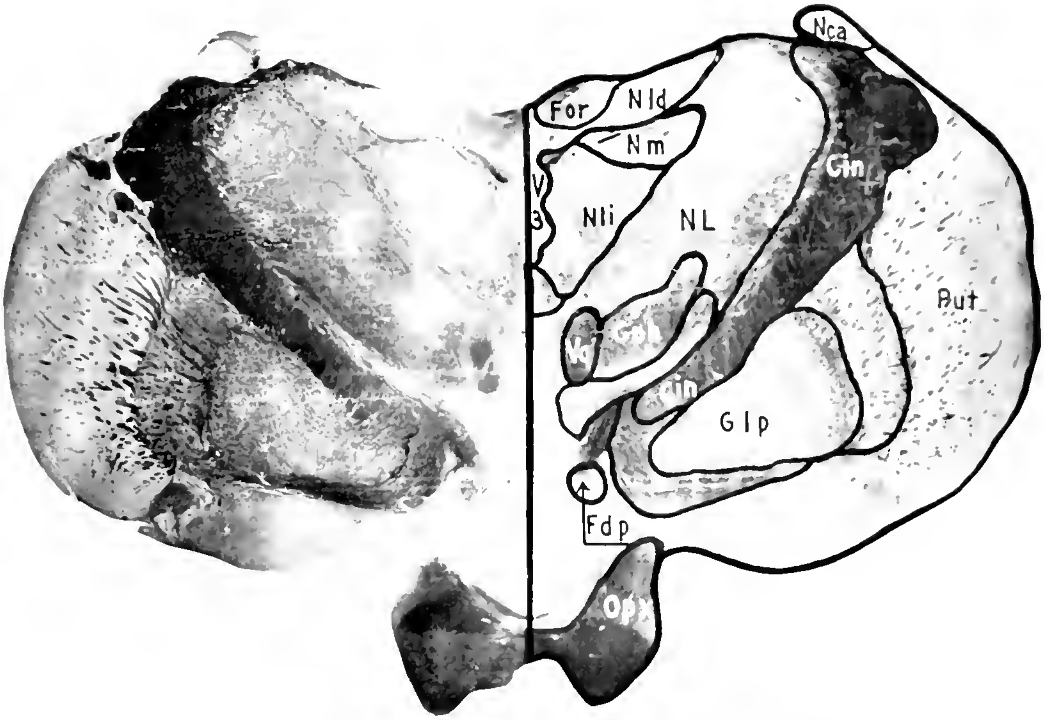


FIG. 310. GORILLA. LEVEL OF THE OPTIC CHIASM.

CIN, Internal Capsule; CPH, Corpus Hypothalamicum; FDP, Descending Pillars of the Fornix; FOR, Fornix; GLP, Globus Pallidus; NCA, Caudate Nucleus; NL, Lateral Nucleus of the Thalamus; NLD, NLI, Internal Lateral Nucleus of the Thalamus; NM, Middle Nucleus of the Thalamus; OPX, Optic Chiasm; PUT, Putamen; VQ, Fasciculus of Vicq D'Azyr; V3, Third Ventricle. [Accession No. J. D. Section 1020. Actual Size 45 × 24 mm.]

In the ventricular floor are the decussating fibers in the optic pathway forming the optic chiasm (Opx). Superposed above the optic fibers is a small specialized bundle of fibers constituting the narrow supra-optic commissure of Meynert. The two optic thalami are separated from the corpus striatum (Glp) by the interposition of the dense mass of myelinated fibers forming the internal capsule (Cin). This section illustrates the process of divergence characteristic of the upper end of the brain stem by which the fibers constituting the two cerebral peduncles establish ultimate relations with the two cerebral hemispheres.

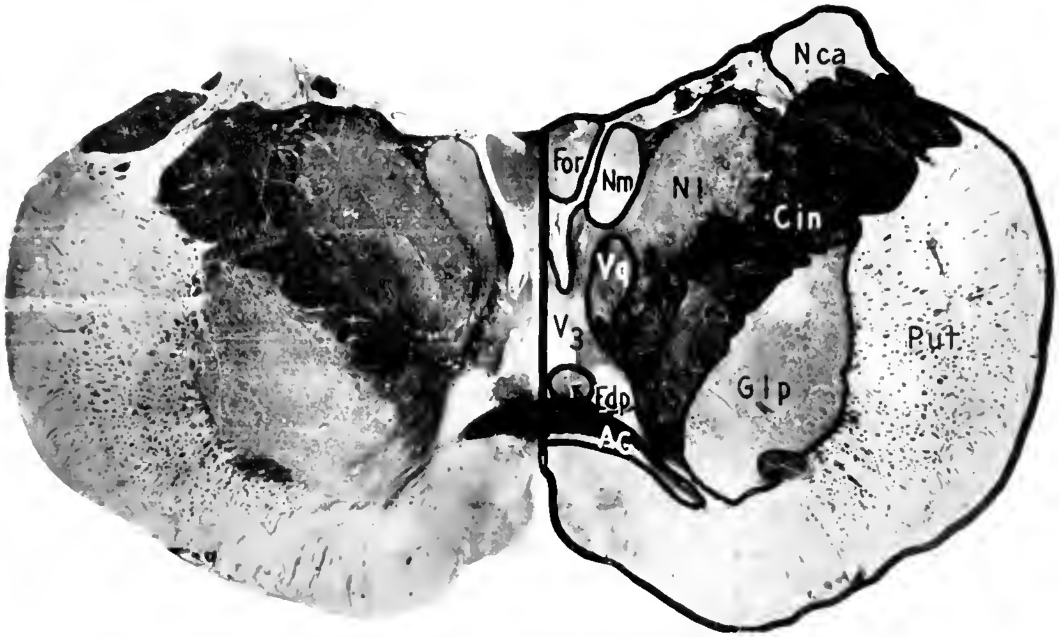


FIG. 311. GORILLA. LEVEL OF THE ANTERIOR COMMISSURE.

AC, Anterior Commissure; CIN, Internal Capsule; FDP, Descending Pillars of the Fornix; FOR, Fornix; GLP, Globus Pallidus; NCA, Caudate Nucleus; NL, Lateral Nucleus of the Thalamus; NM, Middle Nucleus of the Thalamus; PUT, Putamen; VQ, Fasciculus of Vicq D'Azyr; V3, Third Ventricle. [Accession No. J. D. Section 1150. Actual Size 47 × 15 mm.]

LEVEL OF THE ANTERIOR COMMISSURE (FIG. 311)

Here the cephalic extremity of the brain stem presents itself as the much reduced cephalic portion of the optic thalamus. These terminal structures are separated by the internal capsule (Cin) from the lenticular nucleus (Put). The cephalic extremity of the third ventricle appears in the section, beneath which pass the fibers of the anterior commissure (AC). The remaining features in the cross section are indicated by corresponding letters in the caption.

Chapter XXII

RECONSTRUCTION OF THE GRAY MATTER IN THE BRAIN STEM OF TROGLODYTES GORILLA

The High Cervical Level of the Spinal Cord

THE upper level of the cervical cord presents an appearance strikingly similar to that found in the high cervical level of the human spinal cord. In the level at which the reconstruction is begun, the ventral gray columns are still in contact with the central gray matter of the cord. Lateral to the ventral gray column is the small lateral cell column behind which is an area already showing indications of reticular formation. The ventral gray column is here roughly triangular in outline, with its apex directed ventrally. It presents a mesial surface which is more or less parallel with the fellow of the opposite side, a lateral sloping surface and a base which is in contact with the central gray matter.

The cervix and base of the dorsal gray column are both directed ventrodorsally, while the substantia gelatinosa Rolandi which surmounts the dorsal horn and flares somewhat laterally presents a typical primate appearance. As the junction of the high cervical level with the oblongata is approached, the ventral gray column diminishes in size and finally merges with the reticular formation which has increased in size pari passu with the decrease in the ventral gray column.

The substantia gelatinosa Rolandi as it appears to merge with the substantia gelatinosa trigemini gradually assumes the more lateral position characteristic of it in the oblongata.

The reticular formation gradually increases in size in the oblongata and spreading laterally establishes contact with the ventromesial surface of the substantia gelatinosa trigemini. It eventually replaces the ventral gray column and is continuous across the midline with its fellow of the opposite side.

The Dorsal Medullary Nuclei

The first of the dorsal sensory nuclei to appear is the nucleus of Goll which comes into view in the highest cervical sections. It develops as a narrow prolongation extending backward from the surface of the central gray matter close to the midline. Continuous with the dorsal surface of the central gray matter, from which it takes its origin, it rapidly increases in a ventrodorsal direction until it occupies almost the entire depth of the column of Goll. It is compressed from side to side and completely surrounded, except at its base, by the fibers of the column of Goll. As the lower extremity of the fourth ventricle is approached the nucleus begins to shorten in its ventrodorsal diameter, at the same time showing a marked tendency toward the formation of a nuclear outgrowth which resembles the overhanging branches of a tree. As the ventricle opens the nucleus is pressed aside and separated from its fellow of the opposite side. The nucleus of Goll comes to an end shortly above the opening of the fourth ventricle. The nucleus of Burdach appears at a level only slightly above the appearance of Goll's nucleus as a dorsal prolongation from the base of the dorsal horn. This mass of nuclear material increases until it occupies a large part of the column of Burdach with a dorsolateral extension passing laterally and conforming to the surface configuration of the medulla oblongata. This lateral swing is carried so far that the nucleus of Burdach overhangs to a considerable extent the substantia gelatinosa trigemini which is separated from it by the descending root fibers of the trigeminal nerve. The nucleus of Burdach extends upward almost to the level of entrance of the cochlear root, being separated gradually from the floor of the fourth ventricle by the intervention at this point of the vestibular complex.

The nucleus of the substantia gelatinosa trigemini, in the lower pontile levels, presents the constriction found in the other primate forms the so-called waist of the trigeminal nucleus. The nuclear mass continues upward,

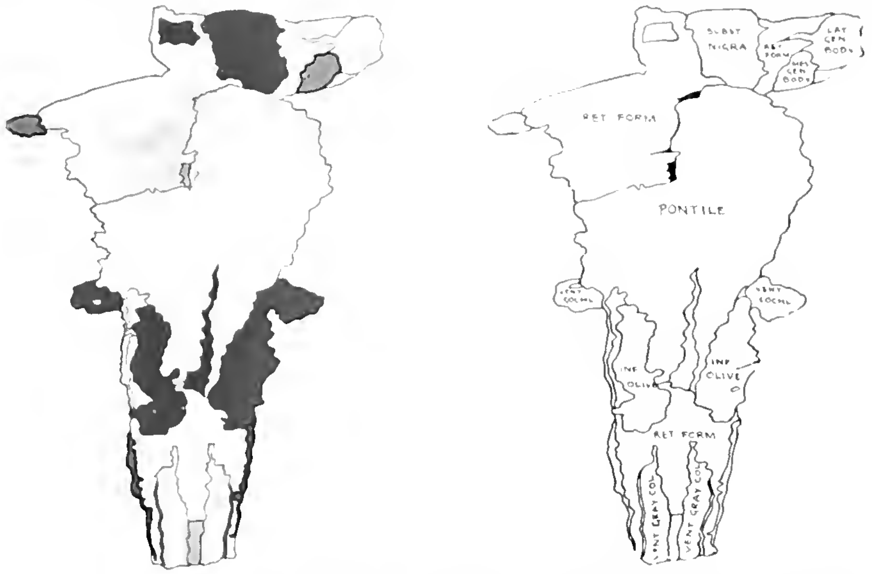


FIG. 312. VENTRAL SURFACE OF GRAY MATTER OF BRAIN STEM, TROGLODYTES GORILLA.

KEY TO DIAGRAM. INF. OLIVE, Inferior Olive; LAT. GEN. BODY, Lateral Geniculate Body; MESO-GEN. BODY, Mesial Geniculate Body; PONTILE, Pontile Nuclei; RET. FORM., Reticular Formation; SUBST. NIGRA., Substantia Nigra; VENT. COCHL., Ventral Cochlear Nucleus; VEN. GRAY COL., Ventral Gray Column.

presenting upon its lateral surface the descending root of the trigeminal nerve, to the mid-pontile region, at which point it expands into its caput. It is here in close relation with the nucleus masticatorius which is situated mesial to the trigeminal caput. Throughout its entire extent the mesial aspect of the substantia trigemini rests in a deep concavity formed in the lateral surface of the reticular formation.

The Inferior Olivary Nucleus

The inferior olivary nucleus first appears somewhat below the level of the opening of the fourth ventricle. Its caudal extremity consists of the chief olivary nucleus (neo-olive). The next portion to appear is the mesial accessory nucleus which is situated ventromesial to the main olivary nucleus. The chief nucleus shows a considerable advance in the complexity of the convolutions and reduplications which characterized it in the chimpanzee. The fundus is broad and presents a number of plications. The dorsal and mesial plates of this nucleus are thrown into extensive folds, while their dorsal extremities turn somewhat inward to run parallel with the median line.

The mesial accessory nucleus of the olive (mesial paleo-olive) appears as a flat band in apposition to the mesial plate of the chief olive with which it is parallel. It becomes continuous with the upper extremity of the mesial plate near the cephalic extremity of the latter. The dorsal accessory nucleus (dorsal paleo-olive) extends along the dorsal surface of the main nucleus embedded in the reticular formation. It forms a narrow band of gray matter with its mesial extremity turned somewhat in the ventrodorsal plane. As the chief nucleus extends upward, the dorsal accessory nucleus becomes continuous with its dorsal plate. The cephalic limit of the olivary nucleus is in the lower pontile region where the nuclear substance gradually disappears by merging with the reticular matrix.

The Reticular Formation

The reticular formation appears in the upper cervical levels situated between the substantia gelatinosa Rolandi and the ventral gray column. It increases in size as it is followed upward, replacing the ventral gray column which merges with it and then extends to the midline to become contiguous at various points with its fellow of the opposite side.

In the lower ventricular levels it supports the inferior olivary complex which is embedded in its ventral surface. The reticular formation is more or less quadrilateral in shape with a ventromesial, a ventrolateral, a dorsal and a mesial surface. The mesial surface faces toward its fellow of the opposite side from which it is separated by the longitudinal fiber bundles situated close to the raphe. These bundles are parallel to the median raphe, so that above the

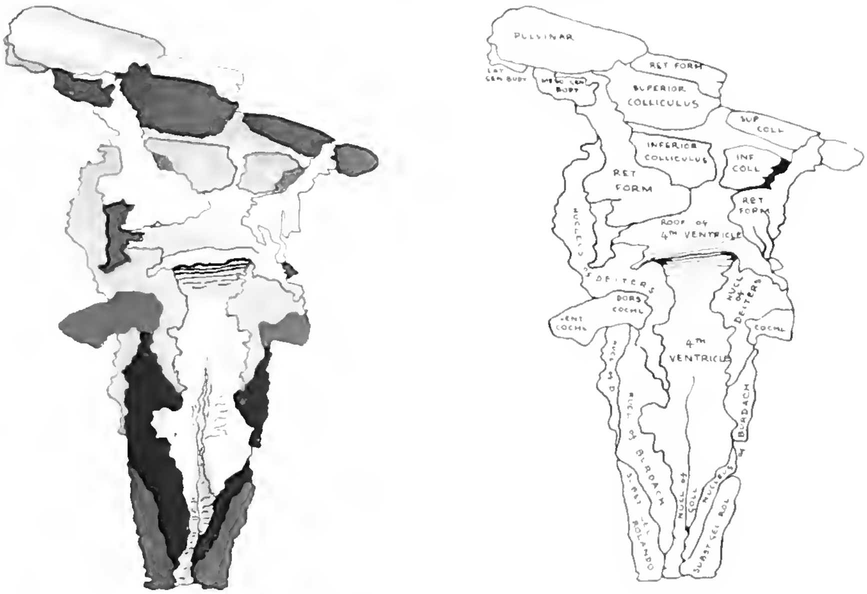


FIG. 313. DORSAL SURFACE OF GRAY MATTER OF BRAIN STEM, TROGLODYTES GORILLA.

KEY TO DIAGRAM. COCHL., Cochlear Nucleus; DORS. COCHL., Dorsal Cochlear Nucleus; INF. COLL., Inferior Colliculus; LAT. GEN. BODY, Lateral Geniculate Body; MESO-GEN. BODY, Mesial Geniculate Body; NUCL. OF BURDACH, Nucleus of Burdach; NUCL. OF D. and NUCL. OF DEITERS; Nucleus of Deiters. NUCL. OF GOLL, Nucleus of Goll; RET. FORM., Reticular Formation; SUBST. GEL. ROL. and SUBST. GEL. ROLANDO, Substantia Gelatinosa of Rolando; VENT. COCHL., Ventral Cochlear Nucleus.

beginning of the olive the right and left sides of the reticular formation are no longer contiguous at the midline.

The ventrolateral surface of the reticular formation appears between the inferior olivary nucleus and the substantia gelatinosa trigemini which is embedded in the dorsal portion of this surface. In the ventrolateral surface are also the nuclear collections which form the lateral nucleus of the reticular formation. They may be followed in an uninterrupted continuous chain almost into the pontile region. The dorsal surface of the reticular formation is in contact with the central gray matter but demarcated from it by the circumferential fiber bundles of the reticular formation.

The reticular formation is a massive structure in the tegmentum of the metencephalon. It provides a matrix in which develop the various nuclear specializations characteristic of the metencephalic tegmentum. It also affords a supportive medium through which pass many longitudinal fasciculi.

In the metencephalon the reticular formation is in contact with the deep layer of the pontile nuclei. Here its ventral surface fuses with the dorsal portion of the mesial and lateral buttresses of the pontile nuclei.

Between these two points of contact with the pontile nucleus, the reticular formation is separated from the basis pontis by longitudinal fiber bundles.

In the upper pontile levels the reticular formation becomes superficial. At the point where the superior cerebellar peduncle begins to sweep forward in the isthmus mesencephali a reticular prolongation extends lateral to the peduncle, between the latter and the surface of the isthmus. This prolongation gradually extends dorsally, covering the superior cerebellar peduncle with a heavy investment of reticular substance. At length the superior cerebellar peduncle is completely surrounded by reticular formation. The cerebellar brachium then passes into a tunnel of the reticular formation which extends toward its peduncular decussation. A similar prolongation of the mesencephalic reticular formation presents itself at the transition of the trapezoid body into the lateral fillet. At first the lateral fillet lies superficially upon the outer surface of the reticular formation. It then penetrates this structure, to pass upward toward the lateral extremity of the inferior colliculus.

These dorsal extensions of the reticular formation form a smooth, continuous layer situated close to the periphery of the brain stem. The ventrolateral reticular angles are continued forward and come into contact with the deep layer of the pontile nucleus. Dorsally these lateral extensions receive the lateral extremities of the colliculi.

In gorilla the mesencephalic reticular formation viewed from above presents an arrangement similar to that found in the chimpanzee. It presents a median nuclear mass which extends to the midline, there to become contig-

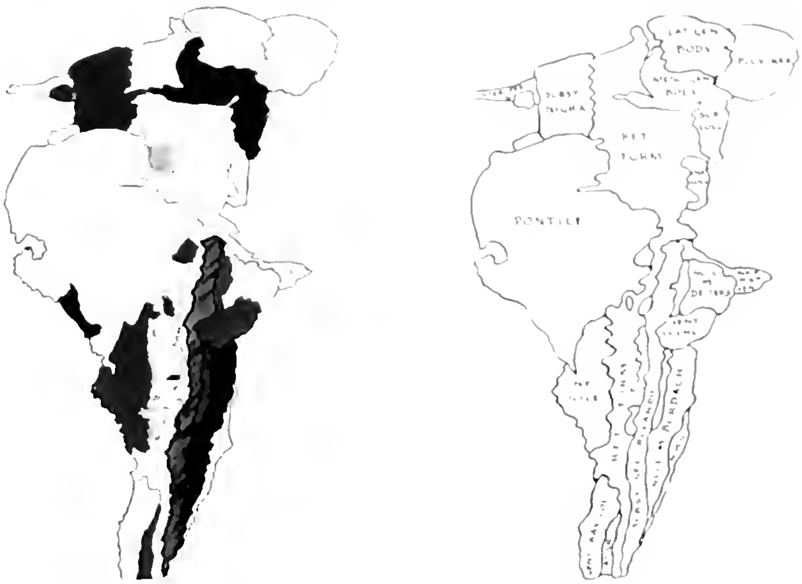


FIG. 314. LATERAL SURFACE OF GRAY MATTER OF BRAIN STEM, TROGLODYTES GORILLA.

KEY TO DIAGRAM. INF. COLL., Inferior Colliculus; INF. OLIVE, Inferior Olive; INTER-PED. G., Interpeduncular Gray Matter; LAT. GEN. BODY, Lateral Geniculate Body; LAT. GRAY COL., Lateral Gray Column; MESO-GEN. BODY, Mesial Geniculate Body; NUCL. OF BURDACH, Nucleus of Burdach; NUCL. OF DEITERS, Nucleus of Deiters; N. OF G., Nucleus of Goll; RET. FORM., Reticular Formation; ROOF OF FOURTH VEN., Roof of Fourth Ventricle; SUBST. GEL. ROLANDO, Substantia Gelatinosa of Rolando; SUP. COLL., Superior Colliculus; VENT. COCHL., Ventral Cochlear Nucleus; VENT. GRAY COL., Ventral Gray Column.

uous with its fellow of the opposite side. The lateral surface of this median mass is serrated and covered by the superior cerebellar peduncle. Lateral to the superior cerebellar peduncle is the dorsal extension of the main mass of the reticular formation which, as the peduncle continues in its course toward its decussation, becomes more extensive.

From the lateral extremity of the inferior colliculus there arises a mass of fibers which produces a hiatus in the formatio reticularis, separating its more ventral portion from contact with the superior colliculus. This hiatus is filled by fibers emerging from the inferior colliculus which collect themselves as a compact bundle—the inferior brachium—and groove the surface of the reticular formation as the tract passes upward to the mesial geniculate body.

A similar arrangement appears in the upper part of the mesencephalon where a mass of fibers emerges from the superior colliculus. These fibers produce a groove on the lateral surface of the reticular formation, passing from the lateral extremity of the superior colliculus to the lateral geniculate body. The fibers constitute a secondary tract in the visual pathway, the superior brachium.

The mesencephalic reticular formation can, in its upper parts, be divided into three main masses: (1) a dorsal mass which lies in contact with the central gray matter, ventral to the colliculi; (2) a lateral portion which forms the most considerable part of the tegmentum of the mesencephalon; and (3) a central portion which gives rise to the condensation of the nucleus ruber. From the mesencephalon the reticular formation is continued upward to merge with the zona incerta of the diencephalon and the indifferent nuclear masses in the caudal-most part of the *interbrain*.

The Pontile Nuclei

The pontile nuclei first appear at levels marked by the lower extremity of the fourth ventricle as the *arciform nuclei*. Here they are disposed along the mesial and ventral surfaces of the pyramidal tract. The arciform nuclei gradually become more extensive, pass laterally and mesially around the pyramidal tract and finally produce a complete investment of that mass of fibers. Proceeding upward they become more extensive, merging with the gray masses of the intrinsic pontile nucleus. They then assume a typical arrangement in a superficial layer and a deep layer. A lateral accumulation of nuclear material forms the so-called lateral buttress, while a similar mesial accumulation forms the mesial buttress. In addition to these, there is developed a distinct intermediate nuclear layer lying between the superficial ventral and the dorsal deep strata. There are also subsidiary layers of gray matter which pass more or less as concentric arcs about the common center from the mesial to the lateral buttress, separating the pyramidal tract and the pallio-pontile fibers into many smaller constituent groups of fibers. This arrangement produces an intricate lace-like appearance in the pontile nucleus. The lateral surface of this nucleus is extremely irregular due to the emergence from it of numerous fiber bundles which constitute the middle cerebellar peduncle. This is especially true in the mid-pontile region where there appears a well-marked hiatus between the intermediate and deep layers of the nucleus. From this opening a large mass of fibers emerges to form the main bulk of the middle cerebellar peduncle.

Cephalically, as the pontile nucleus becomes incomplete along its lateral margin, the mesial buttress is continued upward in contact with the reticular formation to the junction of the hind- and midbrain. At this point the pontile nucleus comes to an end. Its deep layer is continued upward to give support to the substantia nigra. The pontile nucleus is in intimate contact mesially and laterally with the ventral surface of the reticular formation. Between these two points, however, it is separated by longitudinal bundles in the periphery of the tegmental reticular formation. In the mid-pontile region at the point from which the large fiber mass emerges from the pontile nucleus, the deep layer is continued as a definite structure in the reconstruction and can be seen to fuse with the ventrolateral angle of the reticular formation.

The Vestibular Complex

The vestibular complex makes its appearance in the reconstruction as the nucleus of Deiters, here developing in its usual triangular form between the mesial surface of the upper extremity of the nucleus of Burdach and the subependymal gray matter lining the floor of the fourth ventricle.

The Deitersal complex rapidly increases in size and separates the upper portion of the nucleus of Burdach from the central gray matter forming the floor of the fourth ventricle. It also extends rapidly in its ventrodorsal diameter, appearing as a wedge-shaped mass with a triangular extension which overhangs the substantia gelatinosa trigemini. It is separated from the latter by the interposition of the descending root of the trigeminal nerve.

Near the lateral recess of the fourth ventricle the Deitersal complex begins to diminish in size and is replaced by the triangular nucleus of Schwalbe.

Above the region of the lateral recess the nucleus of von Bechterew appears in the lateral wall of the fourth ventricle. The entire vestibular complex extends upward to the mid-pontile level where it rather abruptly begins to diminish and then disappears by merging with the metencephalic reticular formation.

The Cochlear Complex

The cochlear complex consists of the ventral and the dorsal cochlear nuclei. The ventral nucleus presents the regular appearance of a trough receiving the entering cochlear root on its mesial surface, surrounding the nerve upon its caudal, lateral and cephalic aspects. The dorsal cochlear nucleus is situated in the lateral ventricular recess. It is superposed upon the vestibular area and is connected with the ventral cochlear nucleus by strands of gray matter interspersed between the radicular and secondary cochlear fibers. The development of the cochlear complex is about the same as that found in the chimpanzee but appears less extensive when compared with the rest of the gray matter of the stem in most of the lower primates.

The Colliculi

These masses occupy their usual positions in the tectum of the mesencephalon. The superior colliculus is somewhat larger than the inferior colliculus. The latter rests mesially upon the indifferent dorsal gray matter while laterally it is partially supported by the mesencephalic reticular formation. The lateral fillet, as it emerges from the trapezoid body, courses obliquely backward and upward over the surface of the metencephalic and mesencephalic tegmentum. It produces a deep groove in the tegmentum of the mesencephalon as it approaches its destination in the inferior colliculus.

Cephalically the inferior colliculus is separated from the superior colliculus by the dorsal prolongation of the mesencephalic reticular formation lying in the intercollicular furrow. Passing from the lateral surface of the inferior colliculus cephalically and ventrally is a groove produced by the inferior brachium which connects the inferior colliculus with the mesial geniculate body.

The superior colliculus is supported mesially by the indifferent dorsal gray matter and laterally by the lateral prolongation of the reticular formation. Mesially the two colliculi are connected across the midline by the superior and inferior collicular commissures. Cephalically the superior colliculus is continuous with a thin strip of gray matter, a dorsal reticular prolongation, which passes forward to merge with the epithalamic gray matter.

The Substantia Nigra

The substantia nigra appears as a continuation of the dorsal layer of the pontile nucleus. The support derived from the lateral and mesial buttresses, which was so conspicuous in the lower primate species, continues in these higher forms. The substantia nigra presents a ventral surface in contact with the descending pallio-spinal and pallio-pontile fibers. Mesially it is in continuity with the indifferent interpeduncular gray matter. Laterally it is continued outward into rather close contact with the mesial geniculate body, presenting a ventral, hook-shaped prolongation. In this lateral portion is found the specialization in the substantia nigra from which nerve fibers seem to pass into the mesencephalic tegmentum. Dorsally it is concave and separated from the reticular formation by fiber bundles of the tegmentum. Cephalically it extends upward to the junction between the mesencephalon and diencephalon and seems to be continuous with the zona incerta of the interbrain.

The Nucleus Ruber

The nucleus ruber appears in the lower portion of the mesencephalic reticular formation as a rounded nuclear mass, separated from the reticular formation by an encapsulation derived from the superior cerebellar peduncle. It is almost spherical in outline and rapidly attains its maximum diameter, occupying the greater portion of the mesencephalic tegmentum. Passing its level of greatest transverse diameter, the nucleus diminishes and disappears as the mesencephalon begins to assume the characteristics of the diencephalic portion of the brain stem.

The Central Gray Matter

The central gray matter in the high cervical sections of the spinal cord resembles closely that of the human brain stem, being quadrilateral and meeting at its dorsolateral angles the dorsal cornua and at the ventrolateral angles the ventral gray columns. It gradually is drawn dorsally as has been found in the lower forms, giving origin to the dorsal sensory nuclei. As the oblongata is approached the usual narrow prolongation of gray matter passes dorsally around the mesial surfaces of the two tracts of the column of Goll, seeming, as it were, to draw the central gray matter backward toward the dorsal surface of the spinal cord. In this way the central gray matter is flattened out and forms the floor of the fourth ventricle. As the floor opens outward the hypoglossal eminence situated close to its median sulcus and in the most caudal part of the inferior ventricular triangle becomes apparent.

Lateral and dorsal to this eminence is a depressed area which indicates the position of the dorsal vagal nucleus.

The remainder of the floor of the inferior triangle of the fourth ventricle does not show any particular modelling, while in the cephalic half of the ventricle a definite marking is found close to the midline. This represents the position of the nucleus abducentis and the longitudinal, subependymal portion of the seventh cranial nerve. This elevation in the floor is the eminentia teres. It is also known as the eminentia facialis or abducentis.

Lateral to this eminence is a marked prominence in the outer half of the floor of the fourth ventricle. Lying in the lateral recess, it extends for a short distance both cephalad and caudad of the recess. It indicates the position of the dorsal cochlear nucleus.

As the mesencephalon is approached the walls of the fourth ventricle rapidly contract, the roof, floor and lateral walls thicken and converge until the gray matter bounding the fourth ventricle forms a dense mass about the central canal of the midbrain. In the mesencephalon the gray matter is drawn forward ventrally toward the raphe and forms a longitudinal prolongation on either side of the raphe. In this ventral prolongation appear the trochlear and oculomotor nuclei. Above the upper limit of the nucleus oculomotorius the ventral prolongation of the central gray matter becomes more extensive. Proceeding upward this process becomes continuous with the gray matter surrounding the third ventricle and with the median diencephalic nuclei.

Chapter XXIII

COMPARATIVE SUMMARY OF STRUCTURES HAVING EVOLUTIONAL SIGNIFICANCE IN THE BRAIN STEMS OF THE HIGHER ANTHROPOIDS

A Critical Comparison of the Pyramidal Tract, Olivary Nucleus, Dorsal Sensory Nuclei, Vestibular, Cerebellar, Red and Pontile Nuclei, the Midbrain Colliculi and the Oculomotor Decussation: Their Evolutional Significance in Relation to Behavior

1. The Pyramidal Tract in Relation to the Voluntary Control of the Extremities with Especial Reference to the Hand

THE pyramidal system as an index of volitional control affords a consistent guide in estimating certain behavioral differences among the primates. This system of fibers is a distinctly mammalian acquisition. It represents a new adventure in motor organization. In their progressive development the primates have utilized this endowment to greatest advantage. The significance of the pyramidal system is relatively simple. It introduces a new factor into the ancient neural control of the muscles which imparts to their primordial activities a more extensive adaptability. In reality this new mammalian system remodels the old sphere of vertebrate behavior. The animal possessed of it manifests new combinations in reaction, begins to act with some evidence of a wider selection between many possible courses of motor response.

THE NEOPALLIUM OF THE ENDBRAIN

In itself the pyramidal system, however, is but the sublimated representation of the most recently acquired, most expansible portion of the nervous system. This is the neopallium of the end-brain, whose purpose is to create more complex sensory associations as a basis for correspondingly more capable motor reactions. The neopallium is that part of the cerebral cortex which gave the nerve impulse to and supplied the brain power for the age of mammals.

Neokinesis. The neural combinations assembled in the neopallium and projected by the pyramidal system have their externalized expression in an extensive group of reactions collectively known as *neokinesis*. This new type of activity, characteristic of mammalia, is most important because of its potential expansibility. Its limits seem to be set only by the degree to which the neopallium may itself expand. Such extensions as have occurred in this part of the brain may be followed with exactness through all the orders of mammals. They advance step by step through the ultimate transitions observed in the primates and finally reach their culmination in man whose multitudinous neokinetic activities are expressed in the history of the human race. It might be expected that the projection system representing neokinetic development would be a most outstanding feature by which to differentiate the primates, one from another. In general, however, efferent conduction systems in the neuraxis are under the necessity of confining themselves to the smallest possible space. Their purpose is to convey neural impulses already synthetized by more or less extensive central areas and thus ready for transmission to the effectors of the body without further modification or adjustment.

COMPARISON OF THE PYRAMIDAL SYSTEMS IN THE GREAT ANTHROPOIDS

The comparison of the pyramidal systems in the great anthropoids discloses an essential equality in these three infrahuman species. The pyramidal coefficients of all of the higher anthropoids have relatively the same value, although the chimpanzee stands somewhat above either the gorilla or the orang-outang in this regard; so much so that the difference thus established may require explanation. From the known behavior of Troglodytes niger, based on Professor Köhler's studies, the chimpanzee seems endowed with a slightly wider range of neokinetic activity than either of the other great apes. This conclusion might imply a higher degree of intelligence on the part of the chimpanzee, and consequently place the animal nearer to man in the primate series. The inference, however, is not so convincing when the physical limitations of gorilla and orang are taken into account. The great size of the former and its natural ineptitudes for satisfactory arboreal and terrestrial living to some extent at least restrict the range of its adaptability as compared to the smaller, better proportioned, somewhat more active chimpanzee.

The case of the orang is seemingly more difficult to establish, for in general size and body weight, it is more chimpanzee-like. Its physical handicaps, therefore, are not so apparent as those of the gorilla; yet on closer inspection, the underlying reason for its restriction in the acquisition of skilled acts may be discerned. The excessive length of its powerful arm, while admirably adapted to the purposes of arboreal life, seriously limits its usefulness for many other purposes. Thus, although the chimpanzee in its pyramidal system gives evidence of greater volitional control than either the orang or the gorilla, this difference may but express certain superior physical qualities of one form over its closely allied congeners. From this point of view, the conclusion that, because of its greater pyramidal coefficient, the chimpanzee possesses higher intelligence than the orang or the gorilla, seems somewhat doubtful. The differentiation of the forelimb in all three of these forms is about on a par, and the manual development can scarcely be said to give advantages in one or the other. In all three of them the great length of arm cannot be other than a restricting influence in the more plastic and useful adaptation of the hand. Furthermore, the deficiencies in the feet of all of these great anthropoids unfit them for an effectual erect posture and thus impose upon them all alike a limitation which prohibits the ultimate culmination of manual differentiation. Neither the hand nor the foot is exclusively such in the great anthropoids. Each partakes of characters of the other; the foot in many respects being hand-like, while the hand is much used as a foot. The planimetric coefficients of the pyramidal systems in orang, chimpanzee and gorilla are given in the following tabulation:

Planimetric Coefficients of the Pyramidal System in Higher Anthropoids

Species	Coefficient
Gorilla	.161
Chimpanzee	.172
Orang-outang	.160

COMPARISON OF THE PYRAMIDAL SYSTEM IN THE GREAT ANTHROPOIDS AND THE INTERMEDIATE PRIMATES

The general relation of the pyramidal system in the higher anthropoids to that of the intermediate primates is of even greater interest. Whatever slight differences exist among the great apes in this respect, the variation between these and the intermediate group is so striking as to leave no doubt concerning a definite advance in neokinetic organization. The pyramidal system in the higher anthropoids is much greater than in the intermediate primates. The gibbon stands lowest in the scale. Reasons for its more limited neokinetic activity have already been ascribed to the restrictions imposed upon it by its extreme arboreal specialization and its imperfect development of the lower extremity. Macacus, on the other hand, stands nearest to the higher anthropoids, although the interval between it and them is impressive. This approximation may, perhaps, be explained by the fact that the macaque has developed an efficient manual organ which only lags behind that of the higher anthropoids because of the animal's extensive specialization for an essentially arboreal type of life.

COMPARISON OF THE PYRAMIDAL SYSTEM OF THE GREAT ANTHROPOIDS AND THE LOWER PRIMATES

Contrasted with the lower primates, the advance of the pyramidal system manifested by the great anthropoids puts the question of progressive expansion in neokinetic function entirely beyond the realm of doubt. No more striking instance of evolutional progress may be found than that represented by the remarkable disparity in pyramidal development between the lower primates and the higher anthropoids. In only one instance, namely, mycetes, does the pyramidal coefficient even approximate that of the great apes. The lemur and the marmoset are so far distant from the chimpanzee, gorilla and orang in this department of their organization as almost to seem representatives of another order. From this lower limit to the higher one, a steady expansion in neokinesis appears to have exerted an irresistible influence in progressively expanding the sphere of behavioral reaction.

11. The Olivary Nucleus in Relation to the Regulation of Simultaneous Movements in the Eyes, Head and Hand and the Facilitation of All Skilled Learned Performances

The relation of the inferior olivary body to the control of simultaneous movements of eye, head and hand and to the facilitation of coordination of all skilled learned performances, ascribed to this structure in this discussion, should be accepted with certain reservations. In any case, the structural evolution manifested by the olive within the family limits of the Simiidae is beyond dispute. The gorilla presents an inferior olivary body which is considerably larger in its planimetric coefficient than that of either the chimpanzee or the orang-outang. Combined with this advantage in size accredited to the gorilla, other structural features indicate a further specialization in the olive. The degree of convolution and the definition of outline attained by the olivary body are features of utmost importance in determining the differentiation of this structure. In this respect the gorilla approaches most closely to the human standard. Its olivary nucleus is more clearly defined and more complexly convoluted. As compared with the orang-outang, the difference is striking, for in this latter species neither outline nor convolution shows an advanced degree of differentiation.

In size as well as morphological definition, the chimpanzee occupies an intermediate position between the orang and the gorilla, which latter species, for this reason, seems better provided with coordination of simultaneous movements of head, eye and hand. The physiological expression of these morphological conditions may be somewhat difficult to establish, inasmuch as both the orang and the chimpanzee are known to possess very accurate regulation in their oculo-cephalogyric functions. It is probable that the gorilla has not as yet been sufficiently studied by precise scientific methods to justify a statement concerning the relative degree of its development in this important department of neural control. Yet, from what is known of this animal's reactions in captivity, it would seem to possess a high degree of specialization in those delicately adjusted movements of the eye and head for the regulation of the hand in movements of extreme precision. Whether the gorilla has actually a greater manual deftness, a more effectual regulation of those complementary movements in the eye, the head and the hand which practically welds these parts into a single organ (in the physiological sense at least) must await still further examination bearing upon the comparative behavior of these three primates. The measurable differences of the inferior olivary nucleus are shown in the planimetric coefficients of the inferior olivary nucleus for orang, chimpanzee and gorilla as arranged in the following tabulation:

Planimetric Coefficients of the Inferior Olive in Higher Anthropoids

Species	Coefficient
Gorilla	.186
Chimpanzee	.174
Orang-outang	.172

COMPARISON OF THE INFERIOR OLIVARY BODY OF THE GREAT APES AND THE INTERMEDIATE PRIMATES

Whatever significance may be attached to these differences in the higher anthropoids becomes greatly increased by comparing them with the intermediate primates. The inferior olivary body of the great apes has a pronounced advantage in size over the intermediate group. Nor is size alone the only superiority in this comparison. The morphological definition and degree of convolution in the macacus, baboon and gibbon are far inferior to thes aspects of the inferior olive in the larger anthropoids. In one instance only is there any semblance of an approximation to the standard of the great apes namely, in the gibbon. Conditions underlying the olivary differentiation in gibbon have previously been considered. This animal's exacting need of close coordination between eye and hand in its flight-like passage through the trees has already been noted. Even with this exception, the difference is so marked as to dispel any reasonable doubt concerning the evolutional unfold ing in the olivary advance from the intermediate primates to the higher anthropoids.

COMPARISON OF THE INFERIOR OLIVARY BODY OF THE GREAT APES AND THE LOWER PRIMATES

The difference between the great anthropoids and the lower primates in respect to the inferior olivary body supplies the final argument, if such were needed, to maintain that a progressive structural expansion has been in process from the lowly beginning of the primate kind, through its intermediate stages up to its higher differentiations. The planimetric coefficient of tarsius, standing at the lowest extremity of the primate order, is represented by the low value of 4 per cent, while the gorilla's corresponding planimetric coefficient is 18.6 per cent. This difference between the lowest and the highest forms is so decisive as to justify the supposition of an evolutionary progress in the physiological function of the inferior olivary body.

III. The Dorsal Sensory Nuclei in Their Relation to Discriminative Sensibility in the Extremities

THE NUCLEUS OF GOLL

The nucleus of Goll in the three great apes differs in its function from that of the lower and intermediate forms in the fact that the great anthropoids do not develop a tail. Hence an important sensory area of the body has ceased to exist. The absence of this organ should appreciably impress itself upon the development of the sensory elements in the neuraxis designed to receive the afferent influx from the proprioceptors. As among the great anthropoids themselves, the gorilla has developed the nucleus of Goll to a greater extent than either the chimpanzee or the orang. This may in part be due to the slight advantage which the greatest of these primates has in the development of its foot, which is somewhat better adapted to plantigrade locomotion than that of either the chimpanzee or orang-outang. This interpretation is based upon facts already determined concerning the structural features of the gorilla foot as compared with his anthropoid associates. It also takes into account the supposition that the gorilla, because of his great weight, is forced to go much more upon the ground than the smaller, more agile members of his family. This position, however, may not be accepted without some reservations. That locomotion upon the ground has some bearing upon the expansion of the sensory areas, more particularly the tendency to assume the upright posture, is a view which gains some substantiation from the known behavioral reactions of the Simiidae. The planimetric and longitudinal coefficients of the nucleus of Goll, given in the following tabulation, show a fairly distinct advantage in the development of this structure in the gorilla over the other two forms:

COEFFICIENTS OF THE NUCLEUS OF GOLL IN THE HIGHER ANTHROPOIDS

Species	Planimetric	Longitudinal
Gorilla	086	280
Chimpanzee	050	250
Orang-outang	048	270

Considered in relation with the intermediate primates, the nucleus of Goll in the great anthropoids discloses a rather unexpected equality. It might be presumed that with the defloresecence and final disappearance of the tail, the nuclear structures in Goll's column would so materially fall off that there would be a distinct inferiority of it in the higher forms. This, however, does not prove to be the case. The deficiency which the great anthropoids would naturally be expected to show because of the absence of the tail is surprisingly wanting. Therefore, some factors tending to maintain the general equality of this nuclear structure among the intermediate primates and the higher anthropoids must exert a decisive influence. While it is impossible to prove conclusively at present what the exact nature of this factor is, it appears none the less to be embraced in those specializations of the hindlimb for locomotion upon the ground as well as for the assumption of the erect posture. That there is some such modifying influence at work is indicated by a comparison of the gibbon with the greater anthropoids. In this Hylobate form the nucleus of Goll reaches low-water mark, being less in its dimensions than in any of the other primates. The explanation appears to be in the fact that the animal possesses no tail, and has specialized the hindlimbs but little, either for purposes of locomotion upon the ground or for its arboreal locomotion.

Compared with the lower primates, the great anthropoids show something approaching an equality in the size of the nucleus of Goll, although the lower forms bring forward one striking instance to illustrate the neural results of specialization of the hinder portions of the body. In mycetes, the coefficient of Goll's nucleus is greater than in all other primates, and as this is the only form of all those considered which possesses a highly developed prehensile tail, the significance of sensory specialization in this region of the body becomes apparent. The decrease of prehensile function of the tail and the final disappearance of this organ would of necessity occasion a progressive diminution in the nucleus of Goll. Certain adaptive modifications in the feet and legs making provision for one kind or another of specialized locomotion, either in tree life or upon the ground, would reflect themselves quite as much upon this nucleus. In those instances in which the tail appears to play no conspicuous part, the maintenance of the standard dimensions in Goll's nucleus may be regarded as due to factors operative in connection with specialization in the hindlimb and particularly the foot.

But quite apart from the size of this nuclear relay station, emphasis should be laid upon another feature in the dorsal sensory field. The column of Goll, comprising the ascending fibers from proprioceptors in the hind portion of the body, including the tail when present, shows a progressive tendency to decrease in passing from the lower to the higher primates. The actual volume of medullary fibers serving for the purpose of sensory conduction in the column of Goll in lemur compared with gorilla is something slightly less than one-half. This indicates a distinct falling off in the volume of afferent impulses from the lower extremity and caudal portion of the body in passing from the lower to the upper end of the primate order.

THE NUCLEUS OF BURDACH

The nucleus of Burdach likewise presents not a few difficulties as evolutional evidence in the great anthropoids. Estimated merely upon the basis of its size, orang has the advantage over both gorilla and chimpanzee, thus indicating that the former possesses higher manual differentiation. The apparent inconsistencies of such a view are evident at once. To maintain that the orang-outang has a more highly differentiated hand than either the gorilla or the chimpanzee seems untenable by the criteria of our present knowledge. Nevertheless, the differences obtained by actual measurements are sufficiently striking to make this supposition a strong probability. For the time, at least, it may be wiser to accept the conclusion forced by this relative mensuration of the nucleus of Burdach and seek further light which may uphold or disprove it. The planimetric and longitudinal coefficients of the nucleus of Burdach in the great anthropoids are given in the following tabulation:

Coefficients of the Nucleus of Burdach in the Higher Anthropoids

Species	Planimetric	Longitudinal
Gorilla	081	200
Chimpanzee	073	270
Orang-outang	093	270

When compared with the intermediate primates, the nucleus of Burdach in the great apes again shows a somewhat surprising equality. In fact, the size of this nucleus in macacus closely approaches that of the orang, and actually exceeds the dimensions of the nucleus in the chimpanzee and the gorilla. The significance to be attached to this comparative mensuration points to the fact that in at least one of the intermediate primates, influences are operative in the differentiation of the upper extremity which require a high degree of proprioceptive representation in the nucleus of Burdach. The principal influence underlying this development is the specialization of the hand. Extreme degrees of such specialization may occur along several divergent lines. The evidence, therefore, afforded by the nucleus of Burdach as bearing upon manual differentiation must be weighed most critically.

Such testimony as it does produce may be particularly fortunate if it emphasizes the need for careful scrutiny and great caution in accepting the evidence of evolutional structures concerning which there may be any doubts whatsoever.

When the great apes are contrasted with the lower primates, a striking fact comes to light. Mycetes exceeds in the size of its nucleus of Burdach not only all of the great anthropoids, but all other primates as well. This feature has been discussed in the relation of the lower to the intermediate forms. Emphasis has already been laid upon the probable bearing of the high degree of manual specialization consequent upon the animal's possession of an active prehensile tail.

Conclusions to Be Drawn from a Study of the Dorsal Sensory Field

If the conclusions to be drawn from the relative proportions of Burdach's nucleus to the differentiation of the hand in primates are somewhat indecisive, if they leave the question still in need of further investigation, the dorsal sensory field as a whole bears witness which is satisfactory and positive. It makes clear that in passing from the lower to the higher members of the primate order there is a definite increase in the influx of sensory impulses received from the proprioceptors of the upper extremity. In other words, whatever the size of the receiving nucleus in the column of Burdach, the impulses which reach it from the hand and upper extremity progressively increase in volume. This progressive expansion in Burdach's column is so obvious as to leave no room for doubt. A dimensional comparison of the conduction columns in the dorsal sensory field suffices to establish this point. In the lower primates the column of Goll is larger than the column of Burdach. Gradually the column of Goll becomes less than the column of Burdach, which may be understood to indicate a falling off in the relative importance of the sensory conduction system from the hinder portions of the body as compared with the forelimbs. In the great anthropoids this disparity is so marked that the column of Goll is less than half of the size of the adjacent column of Burdach. Such disproportion in favor of Burdach's column may be accepted as valid evidence. Its gradations may be traced through intermediate stages from a condition in which the column of Burdach is distinctly less than that of Goll in the lower primates, to one in which it is much greater, as in the higher species. It is possible that nuclear structures such as those of Goll and Burdach serving as primary relaying stations for sensory afferents, may, without varying much in size themselves, officiate in this capacity even when the sensory tracts associated with them become much increased in volume.

This discussion may appear to absolve the dorsal nuclei by offering certain extenuations for their apparent failure to reflect the effects of adaptive changes in the extremities. It should in no wise depreciate the evidence afforded by the dorsal sensory field itself. The fact that there is a progressive increment in the influx of sensory impulses from the upper extremity, as compared with the lower extremity in ascending the primate series, remains unassailed. Whatever may be the relative size of the primary relaying nuclei of these special sensory systems, the conduction paths leading to them from the proprioceptors disclose a relative volumetric change in conduction capacity. The ratio of the column of Burdach to the column of Goll in lemur is one to one and a half. This ratio in the gorilla and all of the other greater anthropoids is two to one. It is difficult to interpret this increase in the volume of sensory influx on grounds other than the specialization of the upper extremity and particularly of the hand. Significant also is the relative decrease in the sensory influx from the head and face as indicated by the substantia gelatinosa trigemini in its relation to the nuclei of Goll and Burdach. It is apparent from this interrelation that much sensory responsibility has been delegated from the primitively important areas of the head and face in their capacity as directors of locomotion, to the more mobile explorative organ determined by the higher stages of manual differentiation.

IV. The Vestibular Nuclei in Their Relation to the Balancing Mechanism

The problem of maintaining the balance of the body appears to be subject far less to variations according to mode of life than most of the functions in the brain stem which have an evolutional significance. In spite of well-defined differences in adaptation either to arboreal living or something approaching terrestrial life, there are many fluctuating gradients between these two extremes of specialization. All primates alike develop requirements which impose upon the balancing mechanism nearly the same burden. What one species may lack in one particular, it compensates for by over-development in another direction. This reciprocal rise and fall in equilibratory needs is fairly effective in striking a balance for this function throughout the order. Among the great anthropoids, the chimpanzee presents in its Deitersal nucleus a higher coefficient than either the gorilla or orang-outang. In this development the gorilla is not far behind its apparently better balanced confrere; while the orang shows what appears to be a real inferiority in the central control of its balancing mechanism. It seems probable that because of its great length of arm, this latter form has developed less of the tendencies essential to terrestrial locomotion, while both of the other anthropoids have partially adapted themselves to locomotion upon the ground and in some degree to the upright posture. The orang's capability as a tree-dweller has none of the remarkable specialization seen in the gibbon, and although it manages to make the best of its arboreal environment, its locomotion through the trees is relatively deliberate and slow. It has none of the showy agility which characterizes many of the lighter apes and even the chimpanzee.

Mensuration of the entire vestibular area, including the nucleus of Deiters and the nucleus of Schwalbe in the great anthropoids, shows the same relation between them, the chimpanzee having a slight advantage over both of the others, while the orang shows a considerable inferiority in this development. The coefficients of Deiters' nucleus and of the vestibular area in orang-outang, chimpanzee and gorilla are given in the following tabulation:

Coefficients of Deiters' Area in the Higher Anthropoids

Species	Planimetric	Longitudinal
Gorilla	072	140
Chimpanzee	077	150
Orang-outang	053	150

Coefficients of Vestibular Area in the Higher Anthropoids

Species	Planimetric	Longitudinal
Gorilla	142	140
Chimpanzee	157	150
Orang-outang	100	140

COMPARISON OF THE VESTIBULAR NUCLEI OF THE GREAT ANTHROPOIDS AND THE INTERMEDIATE PRIMATES

The comparison of this portion of the neural organization in the great anthropoids and the intermediate primates shows that they are all about on the same plane of development. The balancing mechanism in the gibbon has the highest value of any member of these groups. This applies both to the size of Deiters' nucleus and the vestibular elements in aggregate. The reason for the gibbon's superiority is obvious. Its remarkable adaptation to arboreal life shows to what degree this animal must depend upon a highly organized equilibratory mechanism. When the contrast is made with the lower forms, the great anthropoids appear to be about on a par with these distantly related primates. Notable exceptions must be taken in the cases of tarsius and mycetes which exceed all of the anthropoids in the size of Deiters' nucleus. This high specialization results from the new responsibilities imposed upon the balancing mechanism by the addition to the animal's motor organization of the prehensile tail or its flight-like leaps. Although some variations do occur in the degree of differentiation manifested by the neural elements of the balancing mechanism, this functional activity is in reality a basic and ancient one which has impressed itself upon the entire vertebrate phylum. It has had its chief incentives to expansion in the assumption of those locomotor characteristics which become necessary to lift the body and support it off the ground by means of the extremities.

The motor responses determined by the essential receptors of this activity belong to the most ancient type of mobility called paleokinesis. Although age alone does not necessarily impart inflexibility, it is true that those elements in the nervous system which have the greatest antiquity represent functional needs whose proper satisfaction demands a maximum of structural development. This, for example, applies particularly to such archaic neural control as that regulating respiration, cardiac activity or the reactions of the gastrointestinal tract. Hence the function inherent in the balancing mechanism of the body would need to develop its full quota of efficiency to be of any service whatsoever. In this light it may be claimed that the vestibular complex in the central nervous system of vertebrates is of little value as indicating the evolutional process. To a certain extent there is truth in this view. On the other hand, those peculiar exceptions in which the fundamental organization manifests marked fluctuations either above the usual standard or something below it, have a special significance in the problem of adaptation. They afford illuminating examples of adaptive radiation in highly specialized functional departments of the organism. Far, therefore, from being insignificant as bearing upon the evolutionary process in the primates, the vestibular complex, although it indicates the general conservatism inherent in the equilibratory elements of motor organization, reveals a marked susceptibility even on the part of such archaic structures to influences developed by the irresistible specializing factors of adaptive modification.

V. The Cerebellar Nuclei and Red Nucleus in Relation to the Coordination of Movements, Especially the More Complex Movements of the Upper Extremity

In the matter of coordinative control of the musculature, differences in the equipment of the great anthropoids are not marked. Whatever slight planimetric advantage may exist is in favor of the orang-outang, although the gorilla is close behind it in this specialization. While the basis for this contrast is afforded by the size particularly of the dentate nucleus, it also includes the configuration of the structure. The coefficients of the dentate nucleus in the three great anthropoids are given in the following tabulation:

Coefficients of the Dentate Nucleus in the Higher Anthropoids

Species	Planimetric	Longitudinal
Gorilla	152	.280
Chimpanzee	136	.230
Orang-outang	160	190

IMPORTANCE OF MORPHOLOGICAL APPEARANCES

Conclusions based wholly upon these figures do not give a comprehensive view of the actual differentiation in this part of the central nervous system. Quite as important as the mensuration of the nuclei is their morphological appearance. In two features of the dentate nucleus it is possible to trace a definite unfolding which gains substantiation from the fact that actual expansions are taking place in the lateral cerebellar lobes. The dentate nucleus in the orang-outang shows a relatively low degree of differentiation in so far as its boundaries are concerned. It has a diffuse uncircumscribed appearance which relates it much more closely to the corresponding structure in the intermediate and lower primates than it does to those forms standing above it in the scale. The degree of convolution in the dentate nucleus is considerably inferior to that of man, chimpanzee or gorilla. In comparing the nucleus of the higher primates it appears at once that the orang is the most primitive in morphological organization. This inferiority of the dentate nucleus in the orang corresponds with the conditions in the lateral lobes which have not expanded to the extent seen in the primates assigned to higher positions in this order. The dentate nucleus in the chimpanzee is much more clearly defined than in the orang and has a richer convolutional pattern. On the other hand, there is a primitiveness about its festooning and foliation which easily distinguishes it from the corresponding structure in the human and gorilla brains. If the dentate nucleus in man be accepted as the standard toward which the evolutional process has been tending, it seems reasonable to assign to the gorilla a position immediately below the human type and distinctly above the chimpanzee. This fact in conjunction with the high degree of development in the lateral lobes of the cerebellum implies that the gorilla stands first in the group of the great anthropoids in so far as the coordinative control of its muscles is concerned.

COMPARISON OF THE GREAT ANTHROPOIDS AND THE INTERMEDIATE PRIMATES

When compared with the intermediate primates the great anthropoids show no great advantage demonstrated by mensuration of the dentate nucleus. On the other hand, in morphological particulars it is evident that a great advance has been made in the dentate organization of the orang, chimpanzee and gorilla as compared with the intermediate group. On the basis of measurements, the baboon has a slight advantage over all the great anthropoids.

COMPARISON OF THE GREAT ANTHROPOIDS AND THE LOWER PRIMATES

When comparison is made with the lower primates, all of these larger apes show a distinct advance both in measurement and in configuration of the dentate nucleus. The baboon is distinctly inferior to the great anthropoids in the morphological details of its dentate structure. This portion of the cerebellum which serves as an index of coordinative control affords a basis for estimating the degree to which the extremities have been differentiated. It should not be overlooked that in all primates with the exception of man the various species are equipped with hand-like feet. Their quadrumanal characteristics play an important rôle in favoring the differentiation of hand-like qualities. By diffusing these qualities through all four extremities, however, they retard the more decisive specialization which concentrates manual differentiation in the upper extremities. Upon the basis of mensuration the intermediate primates and the great anthropoids appear to be on about the same plane, so far as manual differentiation is concerned. The finer structural details of the dentate nucleus, on the other hand, as well as the expansion of the lateral lobes of the cerebellum, establish a gradation which places gorilla in the highest position, with chimpanzee, gibbon, macacus and baboon succeeding in the order given. Such conclusions are borne out by the size and morphological definition of another cerebellar index, the red nucleus. This nucleus has a functional significance essentially similar to the dentate nucleus. It is largest and best defined in the gorilla, although its definition and its size in the orang and chimpanzee indicate the high degree to which coordinative control has been developed in these animals. The planimetric and longitudinal coefficients of the nucleus ruber in gorilla, chimpanzee and orang-outang are given in the following tabulation:

Coefficients of the Red Nucleus in the Higher Anthropoids

Species	Planimetric	Longitudinal
Gorilla	.096	.180
Chimpanzee	.086	.210
Orang-outang	.087	.140

This nucleus is larger in all of the great anthropoids than it is in the intermediate primates. The difference in size becomes even more striking when compared with the lower forms. The evidence, therefore, based upon the cerebellar nuclei and the red nucleus indicates a progressive expansion which is consonant with increased coordinative control. Such control is incident to the acquisition of the complex activities determined by the development of the hand.

VI. The Pontile Nuclei in Their Relation to the Control of Skilled Movements, Especially Complex Manual Performances

Few elements in the nervous system afford more convincing evidence of the evolutional process than the pontile nuclei. Their status indicates the degree of expansion in the cerebral cortex, particularly the neopallial portion of this cortex. Contributions to the fiber constituents which reach the pontile nuclei are made by the frontal lobe, the parietal lobe, the temporal lobe and in all probability also from areas of the occipital lobe. The volume of this nuclear mass thus becomes a reliable index of expansion in the cerebral cortex. Like the pyramidal system, the contingents of nerve fibers which connect the cortex with the pontile nuclei are expressive of neokinetic activities. They denote the motor potentialities inherent in the mammal as well as the degree of complexity with which the species is capable of applying its new effector equipment.

The extension of neokinetic possibilities in the higher anthropoids is considerable if judged by the performances of these animals in captivity. It was thought at one time, when the discovery of the extinct Paleopitheeus was made, that this representative of the great apes had sufficient intelligence to make use of flints. This supposition was probably inaccurate, at least in so far as its implication suggested the purposeful employment of implements. On the other hand, there are many reliable records to show that both the chimpanzee and the gorilla do make use of implements. In a crude, ineffectual way, they actually construct accessory means for accomplishing their purposes. The manner in which the chimpanzee learns to manipulate and throw stones as offensive missiles, its use of sticks and bars for thrusting and striking are examples of the point in question. Furthermore the statement that the gorilla, John Daniel, so well understood the use of hammer and chisel that these tools must needs be under concealment to protect the furniture, are all indications of the degree to which skilled motor performances may be developed in the great anthropoids. To find this development accompanied by a corresponding expansion in the pontile nuclei is not surprising. That the gorilla, on the basis of measurement, should appear to be most favored in this regard seems to have no convincing demonstration in the comparative behavior of these animals. The chimpanzee is but little less highly specialized in its skilled motor acts than the gorilla, while both of these species excel the orang-outang. Further opportunity for study of the higher anthropoids may justify the impressions conveyed by the comparative measurements of the pontile nuclei and actually accredit the gorilla with superiority in its acquired motor performances. The planimetric and longitudinal coefficients of the pontile nuclei in gorilla, chimpanzee and orang are given in the following tabulation:

Coefficients of the Pontile Nuclei in the Higher Anthropoids

Species	Planimetric	Longitudinal
Gorilla	.480	.440
Chimpanzee	.400	.440
Orang-outang	.300	.370

COMPARISON OF THE PONTILE ELEMENTS OF THE GREAT APES WITH THE INTERMEDIATE AND LOWER PRIMATES

Whatever small differences may be apparent from these figures, the pontile elements gain added significance when compared with those of the intermediate primates. In this contrast the degree of pontile expansion becomes striking. Concerning the actual neokinetic accessions of the great anthropoids over and above their simian associates in the intermediate group, there can be no room for question. The developments in this department of behavior are readily recognized. Such contrast is even more emphatic when the pontile nuclei of the great anthropoids are compared with those of the lower primates. A superficial survey of these structures in the two groups is sufficient to disclose pronounced differences between them. Upon actual measurement these differences become convincing and the value of the pontile nuclei as evidenced by their progressive expansion stands as one of the incontestable indices concerning the process of evolutional unfolding in the brain.

VII. The Midbrain Colliculi in Their Relation to the Functions of Sight and Hearing

Among the higher anthropoids the differences in the prominence of the inferior colliculus are relatively slight. These structures in the orang and chimpanzee are essentially equal; while in the gorilla the inferior colliculus shows some tendency to further deflorescence. Interpreted in the light of functional significance, this diminution in the auditory colliculus of gorilla suggests that all motor responses to sudden sounds have less of an immediate reflex quality and more of a deliberative element in their execution. Such observations as have been made on the animal, particularly the adult male, would seem to indicate that when disturbed by the hunter, it does not take to immediate flight. It rises up to stand erect, endeavoring to determine the source whence the sounds arise, and having sufficiently informed itself concerning the nature of its danger, often prefers to attack rather than seek safety in retreat. The planimetric and longitudinal coefficients of the inferior colliculus in the orang, chimpanzee and gorilla are given in the following tabulation:

Coefficients of the Inferior Colliculi in the Higher Anthropoids

Species	Planimetric	Longitudinal
Gorilla	111	070
Chimpanzee	132	100
Orang-outang	131	070

COMPARISON OF THE INFERIOR COLLICULI OF THE GREAT APES AND THE INTERMEDIATE PRIMATES

It is, however, when the comparison is made between the great apes and the intermediate primates that the deflorescent process in the inferior colliculus becomes most convincing. The planimetric coefficients in all of the higher anthropoids are less than in the intermediate primates. The general significance of the gradual decrease in size of the inferior colliculus is not difficult to appreciate. It becomes conclusive when the inferior colliculus of the lower primates is compared with that of the great anthropoids. The meaning of this decline is not obscure, for in proportion as the inferior colliculus diminishes in size, by just so much are compensatory expansions provided for the auditory function in the temporal lobes of the cerebral hemispheres. This delegation serves the purpose of affording a wider, more ample region in the brain for auditory associations. It also brings these associations into intimate relation with afferent impulses received from many other types of receptors in the body, and thus makes possible that blending of sensory impressions which forms the basis of broader experience.

COMPARISON OF THE SUPERIOR COLLICULUS IN THE HIGHER ANTHROPOIDS

The comparison of the superior colliculus in the higher anthropoids does not furnish as convincing evidence of the telencephalization of the visual function as does the inferior colliculus with reference to the sense of hearing. In fact, the orang-outang and chimpanzee show the greatest amount of deflorescence in this portion of the midbrain and indicate thereby a greater degree of delegation of function to the visual cortex in the cerebral hemispheres. This places the gorilla at a distinct disadvantage in the comparative sense. It may be that the mode of life of these three species has some bearing upon this apparent inconsistency. Both the orang and the chimpanzee live among the trees, and enjoy a more unrestricted view of their surroundings than does the gorilla, whose visual outlook is much obstructed by the underbrush. Whether this be regarded as a wholly satisfactory explanation for the distinct retardation which the gorilla shows in the telencephalization of its visual function, it seems advisable to accept the coefficients of the superior colliculus as they have been obtained by measurement in the following tabulation, with the suggestions offered in explanation of them:

COEFFICIENTS OF THE SUPERIOR COLLICULI IN THE HIGHER ANTHROPOIDS

Species	Planimetric	Longitudinal
Gorilla	.140	.110
Chimpanzee	125	.130
Orang-outang	124	090

COMPARISON OF THE SUPERIOR COLLICULI IN THE GREAT ANTHROPOIDS AND THE INTERMEDIATE PRIMATES

As compared with the intermediate primates, the superior colliculus in the great anthropoids is considerably smaller. This is likewise the case when comparison is made with the lower primates, with a single notable exception, namely, in the lemur. That animal, in the coefficients of its superior colliculus, equals the gorilla. The meaning of this discrepancy must still be left in doubt, since the special influences which condition visual expansion cannot yet be evaluated as a whole, and many details of the process require further investigation. In the main, the progressive deflorescence in the superior colliculus shows a steady advance in that process which provides cortical representation for visual functions formerly vested in lower midbrain levels, and hence denotes evolutional development.

VIII. The Oculomotor Decussation in Relation to Binocular Vision

The progress in organization of the visual function has also shown a constant advance in the matter of the internuclear decussations and commissural connections of the nucleus oculomotorius. The necessity of such close association in the interest of conjugate eye movements, whose ultimate object is the production and maintenance of binocular vision, has already been discussed. In the case of the great anthropoids, there is the additional light shed upon this field by the researches of Professor Köhler in tests made upon chimpanzee. From these investigations it was concluded that the anthropoid has developed to a considerable extent the powers of stereoscopic visual perception. The gorilla shows the greatest internuclear communication, and appears to be provided with a more ample means to maintain conjugated eye movements. The coefficients of the gorilla and the chimpanzee exceed those of the orang. These coefficients of the oculomotor decussation are given in the following tabulation:

Coefficients of the Oculomotor Decussation in the Higher Anthropoids

Species	Coefficient
Gorilla	.880
Chimpanzee	.860
Orang-outang	.710

COMPARISON OF THE GREAT APES AND THE INTERMEDIATE PRIMATES

More interesting than the comparison of the great anthropoids among themselves is the contrast afforded between them and the intermediate primates. In this, with the exception of the orang-outang, the man-like apes all show a pronounced advance. The macacus apparently has a development in this respect which is equal to that of the orang-outang; while the baboon exceeds the orang and stands next to the chimpanzee in the development of its oculomotor decussation. The gibbon occupies the lowest place in this comparison. The high figure representing the baboon is undoubtedly due to the fact that this animal, as it lives in more exposed places, is in need of rapid visual adjustment to near and distant objects. It is continually on the lookout not only for the approach of danger, but in search of suitable objects for its marauding exploits.

COMPARISON OF THE GREAT APES AND THE LOWER PRIMATES

When comparison of the great anthropoids is made with the lower primates, the real strides in the organization of visual function become apparent. In this particular there exists the striking difference between gorilla and lemur of 72 per cent, between gorilla and marmoset, of 50 per cent, and even the wily mycetes, with all the additional advantages of its prehensile tail, is approximately 20 per cent below the great anthropoids. These differences are too great to leave doubt concerning the expansion which has affected the progressive development of conjugated eye movements in the interest of binocular vision.

Summary

Were it possible to give in summary the relative values of the structural features considered in this comparative review, the place of first importance would undoubtedly fall to the pontile nuclei. Their testimony, as presented in the great anthropoids, conclusively demonstrates a progressive development indicative of expansions in neokinetic organization. To the evidence of the pontile nuclei and the pyramidal system should be added that of the inferior olivary nucleus whose increasing volume and progressive gain in definition denote functional increments in essential accessories to neokinetic development. Likewise, the oculomotor decussation, indicating as it does the degree of organization in ocular conjugation and binocular vision, adds its increasing advantages to the sum of those influences which develop in the interests of neokinetic expansion. The indispensable activity of visual control for the acquisition and maintenance of many skilled movements, contributes the benefits of stereoscopic vision to the direction of finer manual manipulations. And finally, the deflorescence of the mesencephalic colliculi, progressively advancing through the primate order, typifies that unmistakably evolutional process of telencephalization by which functions originally vested in lower segments of the neuraxis gain more expansible representation in those higher levels especially provided by the cortical regions of the cerebral hemispheres.

PART IV
MAN

INTRODUCTION TO PART IV

THE vast differences between man and all other living creatures are manifest in the complexity of human affairs. In size and form of body there are many notable resemblances between man and the apes, particularly the great apes. But here the similarity ends abruptly. Man has created a new world which he strives to control by laws of his own making.

The record of man's accomplishments has been tempered by every heat of emotion, by rabid denunciation, by equally extravagant praise. Obviously, there is a lack of discriminating impartiality arising from inherent embarrassments of a situation in which man finds himself at one and the same time the material and the maker of his own criticisms. Good reasons exist for the difficulty of maintaining a detached attitude in judgment. For, according as the point of view may be religious, philosophical, historical, scientific, artistic or economic, the incentive force behind the multitude of human activities is ascribed either to the soul, to the psyche, to the mind, to the spirit of man or to human genius.

In the light of history and contemporaneous advancements, it is essential to assume the existence of some specific power which distinguishes man among all living things. But if this assumption disregards the probable genesis of so remarkable a power, it may omit an important detail in the process whereby this striking differentiation has been attained. Were it possible to behold man toiling upward over the long stages of his slow progress during the past half million years or so, this genesis might be the more readily traced. It might be seen in the gradual specialization in those parts of his organization, his hands, with which he has continued to reach out and finally to lay firm hold upon the psyche or soul. This surpassing endowment, Professor Osborn believes, came to man at some critical period when he stood up in the dawning glory of his Cro-Magnon manhood and drew upon the walls of his cave the first imperishable record of his greatness.

Chapter XXIV

FROM PRIMITIVE TO MODERN MAN

Primitive Man—His Times and Personality

THE length of time during which man has inhabited the earth offers a subject for dispute and much difference of opinion. All authorities, however, are agreed that several stages of human progress must have required the passage of a relatively long period. None of the modern estimations of this period is less than 500,000 years. Many calculations, such as those of Sir Arthur Keith, far exceed this figure and place the origin of man as far back as a million years or more. The beginnings of the human species are usually attributed to the early part of the Pleistocene, or even the late part of the Pliocene. Keith, however, does not believe that this permits of sufficient time for the evolutionary process which so evidently has produced all of the effects evidenced in the known features of modern man as well as those of certain extinct varieties of mankind which have long since passed from the stage. Keith concludes his famous work on "The Antiquity of Man" with the statement that "there is not a single fact known to me which makes the existence of the human form in the Miocene period an impossibility."

THE FAMILY OF MAN

Man, in all of his races, both living and extinct, constitutes the sixth family of the suborder of Anthropoidea, known as the Hominidae. This family departed from the common stock representing the orthograde stem of the primates at some time early in the Oligocene. At that critical juncture, probably twenty-five million years ago, two great branches of the suborder parted company. Thenceforth they continued their further differentiation

PITHECANTHROPUS ERECTUS

PILTDOWN MAN

NEANDERTHAL MAN

CRO-MAGNON MAN

FIGS. 315, 316, 317, AND 318. FOUR EXTINCT RACES OF PREHISTORIC MAN. FROM RECONSTRUCTIONS MADE BY PROFESSOR MCGREGOR. IN THE HALL OF THE AGE OF MAN, AMERICAN MUSEUM OF NATURAL HISTORY.

independently of each other. The first of these branches gave rise to the great modern anthropoids in the family Simiidae, including the orang-outang, the chimpanzee and the gorilla. With them also were connected at least two extinct forms, i.e., Dryopithecus, a large gibbon-like ape in many ways resembling the surviving members of this group, and Paleopithecus which made its appearance at a much later period. The second branch to leave the common stem gave rise to the human family. It is to-day represented by all of the modern races of man known collectively as the species Homo sapiens. This species comprises the African, the Australian, the Mongolian and the European varieties.

Keith has graphically illustrated this conception concerning the derivation of the human race from a common prehuman stock as shown in Figure 189 in his work, "The Antiquity of Man." He has also given a like presentation with reference to the derivation of the great anthropoid apes, showing their probable relation to the prehuman stock.

PRIMITIVE RACES WHICH HAVE DISAPPEARED FROM THE EARTH

Paleontological investigations have revealed the former existence of at least four prehistoric races of men who occupied their places upon the human stage for a greater or less period and then, in consequence of factors not yet altogether clear, became extinct. These extinct races appear to vary so considerably from the modern representative of the species that a question has been raised concerning the wisdom of creating for each of them a new genus within the family. One reason for this distinction is that none of the extinct races may properly be considered the direct ancestor of living man any more perhaps than the existing genera of great apes.

Pithecanthropus Erectus. The oldest, most primitive of these races that have disappeared from the earth is known as Pithecanthropus

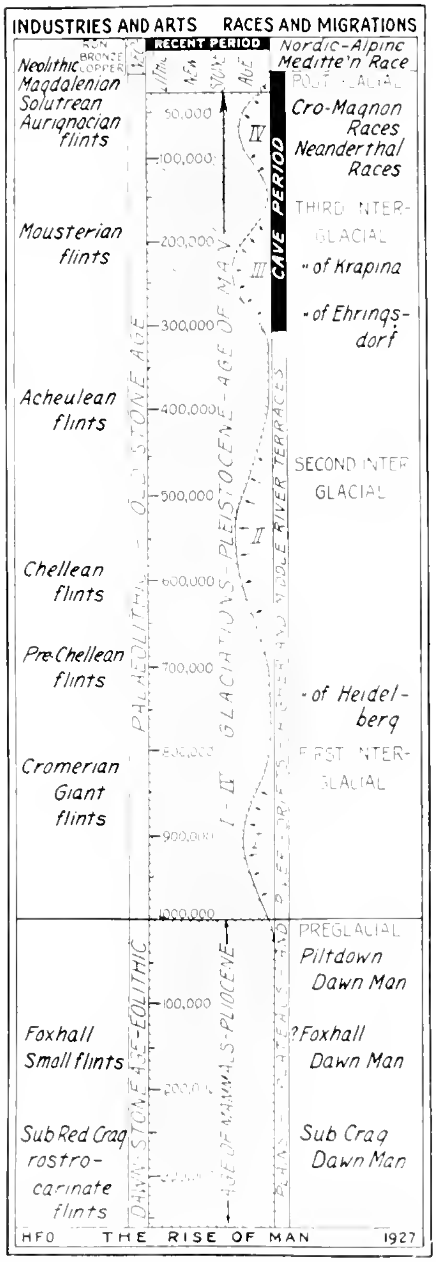


FIG. 319. TABULATION SHOWING PROFESSOR OSBORN'S LATEST ESTIMATES OF MAN'S ANTIQUITY, HIS INDUSTRIES, ARTS AND RACES.

The rise of man is attributed to the Pliocene Epoch. The beginning of the cave period is indicated at approximately 300,000 years ago.

erectus, the Java man of the Trinil race[1] (origin, according to Keith, over one million years ago). This ape-man, although definitely human in type, had so many simian qualities and so much characteristic of man as to justify the view that he represents a transitional stage in human evolution. That he possessed a head and a face not unlike that of an ape with a brain considerably larger than that of any known simian, there seems to be no doubt.

Concerning the detailed organization of this earliest forerunner of the human race, little can be said since his discoverer, Dr. Eugen Dubois, was fortunate enough only to recover several teeth, a portion of the calvarium and one femur. From these fossil remains, however, Dubois has maintained, and other authorities unanimously sustain his argument, that Pithecanthropus erectus, by virtue of the size and shape of his femur, must have assumed the erect posture. He was thus able to walk upon both feet much in the manner of his modern successors. It is also probable that in stature this primitive man was not greatly inferior to the present human races. That he employed his hands in the use of weapons and certain crude implements, that his life depended mainly upon recourse to primitive means for protecting himself against the numerous enemies which beset his path and lay in wait about his camping places, seems more than likely. His time was doubtless so fully preempted by the arduous tasks of gaining sustenance for himself, that little remained for the more leisurely production of ancillary industries or cultural pursuits.

So closely was this human creature related to his contemporaries in the animal kingdom that he managed to hold his position among them only by a narrow margin of superiority. This slight ascendancy was derived from a dawning ingenuity which enabled him to equalize the struggle by the cunning of his hand. Thus he took advantage of primitive shrewdness and contrivance to outwit those natural antagonists which in strength and in speed far

[1] Osborn's chronological estimates are followed in this text.

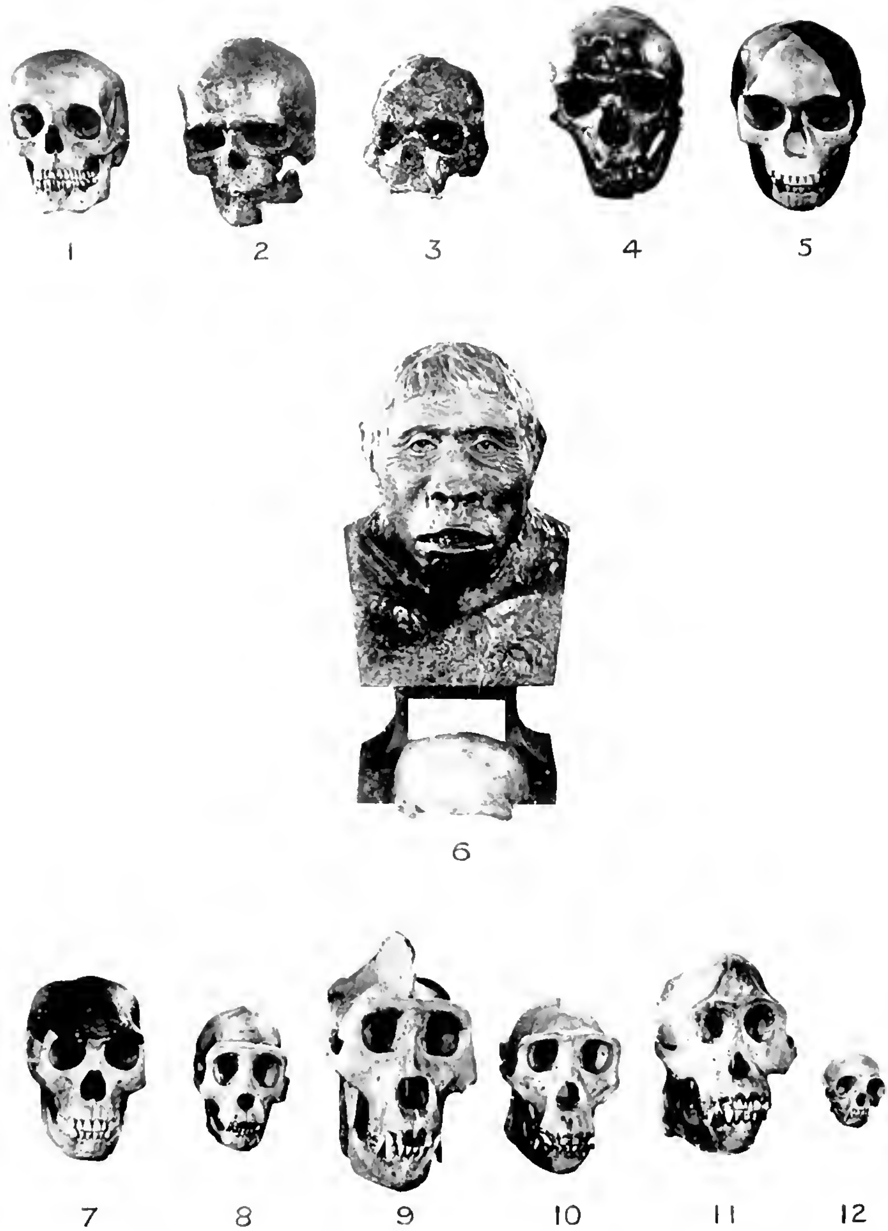


FIG. 320. RESTORATION OF PITHECANTHROPUS ERECTUS BY PROFESSOR McGREGOR COMPARED WITH HUMAN AND ANTHROPOID SKULLS.

1. Homo Sapiens (Modern Existing Type). 2. Cro-Magnon (Fossil Man Equal to the Highest Existing Human Race). 3. Cast of Fossil Skull Found at Taglai, Australia. 4. Neanderthal Man (Lower than Any Existing Race). 5. Piltdown Man (Prehistoric Man of Sussex, England). 6. Pithecanthropus Erectus (Javan Ape-man). 7. Skull of Javan Ape-man Restored from Cast of the Fossil by Professor McGregor. 8. Skull of Young Gorilla. 9. Skull of Adult Male Gorilla. 10. Skull of Adult Male Chimpanzee. 11. Skull of Adult Male Orang-Outang. 12. Skull of Gibbon.

exceeded his limited powers. However humanoid Pithecanthropus may have been in respect to the posture of his body and the general character of his locomotion, it is certain that he was much below any of the known races of man in the capacity of his brain case. It has been estimated that his brain did not much exceed 940 gm. in volume. This is considerably lower than the human standard for the brain, but at the same time it is considerably above the greatest volume of any of the higher apes. His head and face and skull were also subhuman, each having a closer resemblance to the ape than to man. It is possible and even probable, according to the configuration of the brain, that Pithecanthropus had acquired some mode of speech, primitive no doubt and yet sufficient for purposes of rudimentary communication. It is likewise probable that his life took form in tribal organizations, and being gregarious he had learned some of those social and economic advantages accruing from living in community. He may have had some crude notion of the division of labor and its compensations in sharing the results.

Paleoanthropus Heidelbergensis and Homo Neanderthalensis. At some time early in the Pre-Paleolithic, certainly much later than the origin of Pithecanthropus erectus, another race of man made its appearance and has come to be known as Paleoanthropus heidelbergensis, or man of the Heidelberg Race (Homo heidelbergensis). His antiquity is variously estimated at 350,000 to 450,000 years. He too has been described as the possible ancestor of the human stock. Although he manifested many traits definitely more human than Pithecanthropus, the Heidelberg man still must have been a most primitive creature. It is believed, however, that he made use of crude instruments both of wood and stone from the variety of implements found in the neighborhood of his fossil remains. But he, like Pithecanthropus, was doomed to extinction, and no traces of him are found which indicate his survival much beyond the earlier stages of the Lower Paleolithic (250,000 years ago).

What momentous influences, what changes in environment destroyed these two extinct races of man are not clear. The fate which befell them both reveals plainly that, due either to certain inherent defects or to the advent of a new and superior race, they were no longer fitted to survive. If Pithecanthropus, the Java man, was too ape-like in jaw and brain to be considered as the direct ancestor of man, Paleoanthropus, the Heidelberg man, also had definite simian affinities both in jaw and teeth, which appear to exclude him from the ancestral line of modern man.

Although the Heidelberg race became extinct before human progress had made any great advance, there are many facts which indicate that these primitive men were the forebears of another race called Homo neanderthalensis or Homo primigenius which imparted a decisive impetus to the process of human evolution. Neanderthal man has left many more traces concerning his activities in the way of paleolithic implements. By these it is evident that in the organization of his life he had made long strides forward in the direction of his more modern successors. The advances of his industry and his cultural development laid the foundations for all of the stages which progressively evolved as the human race rose in succession through the Old Stone Age to the Neolithic. Finally, by its mastery over the metals, the race acquired that great constructive genius by which it has gradually readjusted the surface of the earth to the greater convenience and comfort of man. And yet Neanderthal man was not, in all probability, the ancestor of the modern races. His skull was too ape-like to permit of such ancestral relation. The size of his brain, however, and the general structure of his body were sufficiently advanced to be in harmony with the requirements of Homo sapiens.

Eoanthropus Dawsoni. In part contemporaneous with both Pithecanthropus erectus and Homo heidelbergensis, and inhabiting the earth with them, perhaps separated by great geographical distances, perhaps from time to time in conflict with them, a third race of man made its appearance at some

FIG. 321. RESTORATIONS OF HEIDELBERG AND PILTDOWN MAN BY PROFESSOR MCGREGOR.

1. Homo Heidelbergensis. 2 and 2A. Reconstructions of Piltdown Man. 3. Restoration of Piltdown Skull.

period in the lower Paleolithic. In many respects it approached nearer to the type of the modern race than either of the other two. This third race of the lower Paleolithic is known as Eoanthropus dawsoni, the Piltdown or dawn man. His fossil remains were found in Sussex, England. By some he is regarded as the direct ancestor of Homo sapiens, by others he is held to be an independent branch of the human family of quite unknown relations to all other races.

CHARACTERISTICS ESSENTIAL TO A COMMON PROGENITIVE STOCK

With Pithecanthropus, Heidelberg man, Eoanthropus, the Piltdown and Neanderthal man thus eliminated as the direct ancestors of the human race as it exists to-day, it must be admitted that evidence of a common progenitive stock is entirely missing. Such a stock must have been much more generalized in type, resembling, for example, some of the more primitive extant races. Perhaps it was not unlike the primitive Tasmanians, whose last surviving representatives passed away within the last half century. Keith believes that of all the races of mankind now alive, the aboriginals of Australia alone could serve in such ancestral capacity. This common ancestor must needs produce descendants which, on the one hand, might become the typical inhabitant of central Africa and, on the other, the fair-haired native of northwestern Europe. The Australian aborigine has those intermediate and generalized characters needed for such an ancestral form. If it be agreed, therefore, that he or some other primitive race of like kind was the common ancestor of the white and black races, it is apparent that a long period of evolution would be necessary to produce such divergent descendants as the negro and the European. For this reason, Keith believes that the period concerned in this differentiation must have been at least as long as the entire Pleistocene. Indeed, this hardly seems sufficient for the purpose. Such an estimation consequently places the more primitive forms of man, as Pithecanthropus, further back than is usually conceded to be the case. It is Keith's opinion

FIG. 322. THE NEANDERTHAL RACE.

1. Original Type of Neanderthal Race Discovered Near Dusseldorf in 1856. 2. Spy Skull II (Neanderthal Race) Resembles Dusseldorf and La Chapelle Skulls. 3. Spy Skull I (Neanderthal Race). From the Collection of Mr. J. Leon Williams. 4 and 4A. Reconstructions of Neanderthal Man by Professor McGregor. 5. Cast of Neanderthal Skull (La Chapelle-aux Saints) Restored by Professor McGregor with Injuries Corrected and Teeth Replaced. 6. Cast of La Chapelle-aux-Saints Skull Discovered with Mousterian Flint Implements in 1908. 7. Restoration of La Quina Skull (Neanderthal Woman).

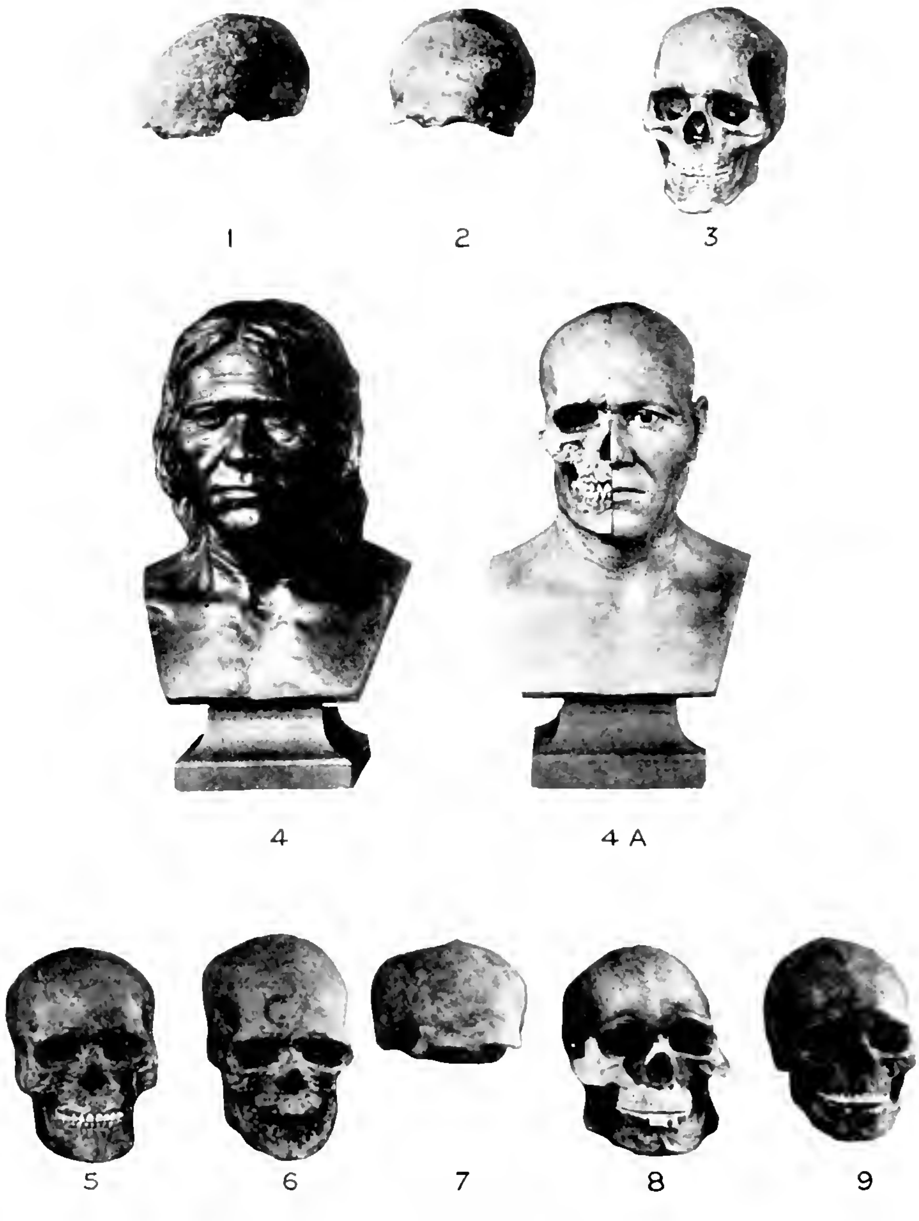


FIG. 323. THE CRO-MAGNON RACE.

1 and 2. Cro-Magnon Calvaria. 3. Cast of Combe Capelle Skull (Homo Sapiens Aurignacensis). The Original Was Found Near Montferrand, France. 4 and 4A. Reconstructions of Cro-Magnon Man by Professor McGregor. 5 and 6. Homo Sapiens Cro-Magnonensis Found at Les Eyzies in 1868. 7. Calvarium of Cro-Magnon Race. 8. Restoration of Cro-Magnon Skull from a Study of Other Skulls of This Race. 9. Replica of Cro-Magnon (Woman) Skull and Mandible.

that the Java man may represent a Miocene rather than a Pliocene stage in human evolution.

PRIMITIVE MAN AS REVEALED BY THE WORK OF HIS HANDS

However difficult the problems of man's ancestry, however fragmentary the skeletal proofs of his antiquity, one phase of his prehistoric existence offers a fertile field for research in the endeavor to discern his lineaments so greatly dimmed by the past. The use of certain extracorporeal agencies must have been the secret of his first real successes in the conquest of the earth. As he first began to manifest the attributes of man through the arts and industries of manual contrivance, as he passed slowly from one stage to the next, what record of himself has he left in the way of the implements by means of which he achieved his ultimate successes?

Primitive Man—His Cultural Phases

Man's obscure beginnings are all but lost in the great geological ages which lie behind his recorded history. To comprehend this vast extent of time, whether it be something more or less than a million years, is enough to baffle the most facile imagination. Little wonder that such insignificant traces of his remains have yet been brought to light. Doubtless when the search becomes more extensive and more thoroughly organized, further signs of his primitive structure and activities will be discovered.

Quite as important as the morphological remains of prehistoric man are those works of his hand, which have been slowly accumulating as the result of untiring patience and geological research. It is now possible to classify this great body of evidence in such a way as to show the existence of certain industrial and cultural stages through which man has passed prior to his actual historical period. That he began as a nomadic hunter, slowly acquired the crude essentials of manufacture, gradually developed the dexterity and

Courtesy, American Museum of Natural History

FIG. 324. STONE IMPLEMENTS REPRESENTING THE SEVERAL STAGES OF PALEOLITHIC CULTURE FROM THE CRUDEST TO THE MOST REFINED PHASES OF THE OLD STONE AGE.

esthetic sense of the artist, and finally learned the practices of agriculture, more or less definitely set the industrial formula according to which he developed implements adapted to each of these pursuits. His past has therefore been subdivided into periods characterized by the presence of implements indicating these specialized activities. The several periods bear the names of French stations or towns near which the discoveries of the implements have been made. Here the French archeologists have so successfully devoted themselves to the effort of bringing order out of chaos that they have established a chronology which is accepted as a working basis of the evolutional progress of man's activity in the long periods of his prehistoric existence.

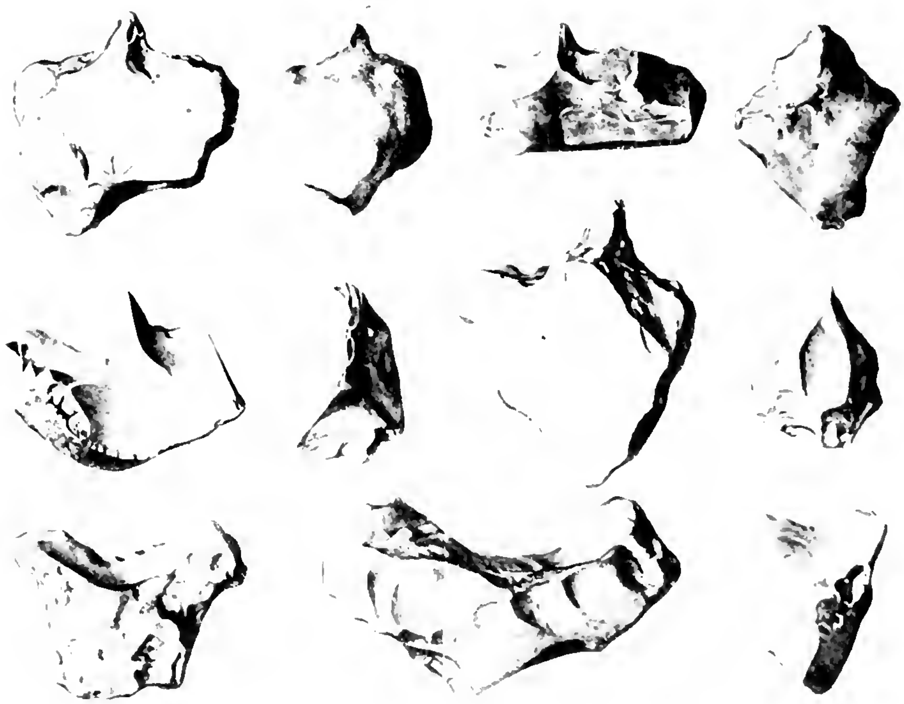
CULTURAL PURSUITS OF THE MEN BEFORE THE OLD STONE AGE

Man's first great epoch on earth was the *Paleolithic* or the Old Stone Age. In this era, which began at some time in the First Interglacial Period, his sole implements were those devised from flint or other kinds of stones, wood, carved ivory and bone. Two subdivisions of this age are recognized in the Lower Paleolithic and the Upper Paleolithic. The Old Stone Age was followed by the *Neolithic* which began in postglacial times, and then came the productive transitional eras which led rapidly up to the thresholds of history through the Bronze and Iron Ages.

PRE-PALEOLITHIC MEN. Long before the beginning of the Old Stone Age, at some time during the First Glacial Period (beginning 1,000,000 years ago), the oldest known representative of human kind had lived upon the earth. It was his fossil remains which Dr. Eugen Dubois discovered in Java that led to the recognition of this Trinil race, now technically known as Pithecanthropus erectus. Little may be said of his cultural development, although some authorities believe that he made use of the very primitive implements called eoliths.

CULTURAL STAGES OF THE OLD STONE AGE

The Upper and Lower Paleolithic periods are further subdivided according as the evolution of manual dexterity makes itself apparent in the implements employed by man. His instrumental equipment was at first extremely simple and crude. But in time there came an increasing complexity and much refinement in all of his tools. These implements clearly indicate a slow but progressive growth in the application of extracorporeal agents which at length made him master of the inanimate and living world.

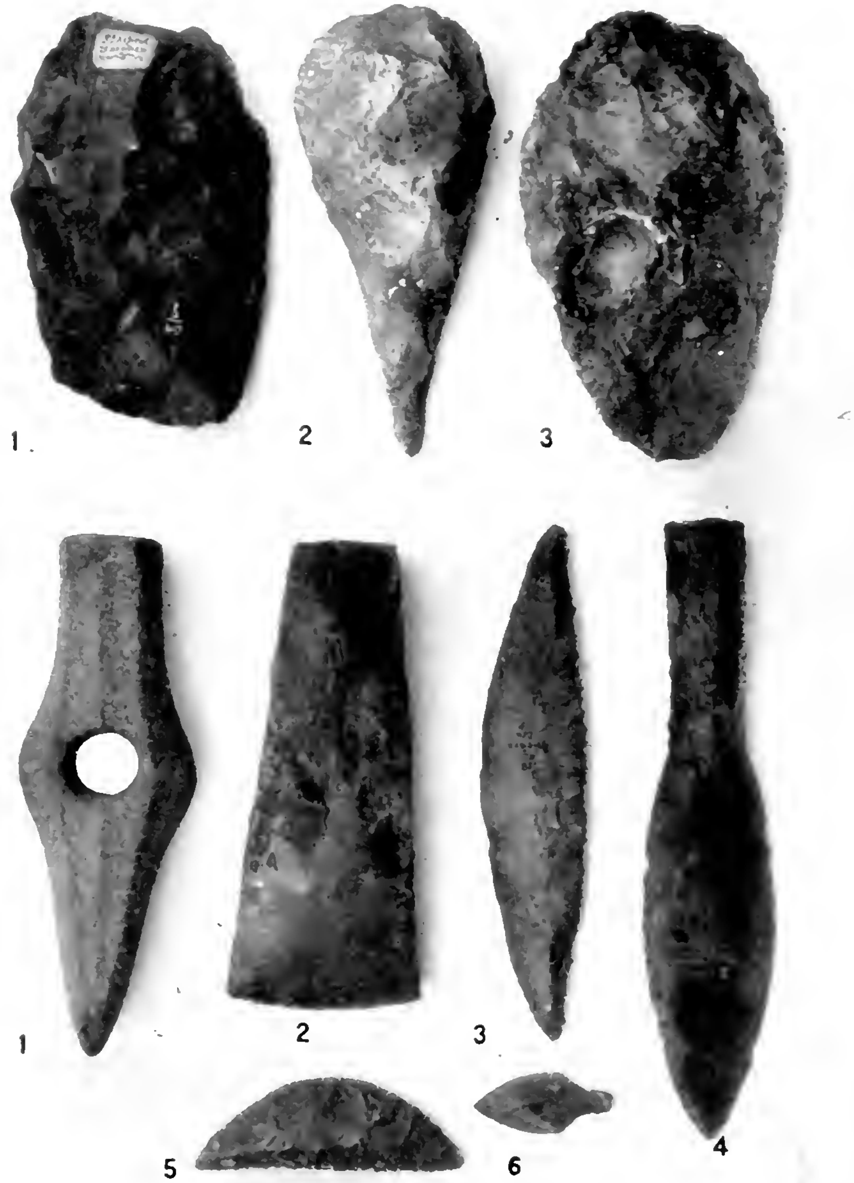


From Quart. J. Geolog. Soc., lxix, Plate xvii

FIG. 325. "EOLITHS" FROM PILTDOWN, SUSSEX, SUPPOSED TO REPRESENT THE EARLIEST STONE IMPLEMENTS, SO CRUDE IN APPEARANCE AS TO BE FREQUENTLY TERMED "ACCIDENTAL FORMS."

Pre-Chellean Cultural Stage. The earliest period in the Lower Paleolithic, the *Pre-Chellean* (beginning 700,000 years ago), is characterized by the use of most simple and primitive stone implements. The chase is represented in this period almost exclusively by the knife (couteau). War, apparently, was not among man's then highly organized pastimes for he appears to have possessed none of those implements which later became such conspicuous products of his handiwork and so essential to his existence. His flint knife was crude, but sufficient with his other equally crude combinations of stone and stick to furnish him a slight balance of power in dealing with his infrahuman competitors, to gain his daily food, and to establish that footing from which he rose step by step. In this period he had also invented for his industrial and domestic purposes a flint scraper (racloir), a planing tool (grattoir), a drill or borer (perçoir) and a stone hammer (percuteur). Nothing among his primitive implements appears to have answered the purposes of art or artistic production, nor had he yet learned the practice of using bone for the preparation of instruments applicable either in the chase or in domestic industries.

The life of this Pre-Chellean man was that of the vagrant hunter, living without the protection of habitation and thus exposed to the devastations of the great carnivores which stealthily followed his wanderings. There is little to show that he had acquired sufficient constructive ingenuity to protect himself against these great predacious marauders which stalked him in his marches by day and lay in wait on the outer edges of his encampments to find him an easy prey as he slept by night. The less fortunate members of his tribes were easily accessible to the night prowlers waiting only for the darkness to assist them in the capture of their human quarry. His slow and inelastic imagination required ages to show him that he held within his own hands the power to repel and subjugate the beasts of prey which almost with impunity made ravages upon him in his unprotected state. How long he struggled upon this low level of intelligence, living a hand-to-mouth existence,



Courtesy, American Museum of Natural History

FIG. 326. CONTRASTS BETWEEN IMPLEMENTS OF THE PALEOLITHIC AND NEOLITHIC AGES.

Upper Row, Paleolithic. 1. Hand Ax. 2. Dagger. 3. Scraper.
Lower Row, Neolithic. 1. Ax and Hammer with Perforation for Shaft. 2. Partially Polished Ax. 3. Saw. 4. Dagger. 5. Knife. 6. Arrow Point.

passing his days in a life not unlike other animals of field and forest, with little recollection of the happenings of yesterday and almost no thought for the morrow, a creature whose mental processes shut in so closely behind him as almost to exclude the experience of the past as a teacher for his future, cannot be estimated in definite epochs of time. There was little inherent in his psychological processes that seemed to give promise of further expansive development in his adaptations. Doubtless some critical incident, like the discovery of fire and its uses, may have furnished a new incentive for his advance. A great change in climate with increasing cold may have forced him into greater physical exertions as a more assiduous hunter of animals for the warmth to be had from their protecting skins. Long winter seasons when game was scarce may have taught the wisdom of storing his supply of provisions and thus aroused in his imagination some conception of the advantages in thought for the future.

Heidelberg Man (Pre-Chellean). At some time in the Second Interglacial Period (beginning about 700,000 years ago) a type of Paleolithic man appeared who seemed possessed perhaps of a more progressive spirit and a definitely increased capacity for adaptation to varying conditions in his environment. His cultural characteristics during the later stages of his slow development merged into those typical of the Pre-Chellean. What relation this Heidelberg race of men bore to those early ape-like humans of the Pithecanthropus variety is not yet understood. It is probable that both were offshoots of the same common progenitive stock, and thus only distantly related. The Heidelberg men were the first human race to inhabit western Europe. They made their appearance in northern Germany approximately 350,000 years ago, and lived in the midst of an imposing mammalian fauna, for the most part of northern aspect. Among these were the lion, the wolf, the bear, the deer and the wild boar, while on the plains lived the Etruscan rhinoceros, the Mosbach horse and the ancient elephant. This race, known as Paleoanthropus heidelbergensis, although possessed of a low psychic organization showed a certain advance over its earlier human predecessors. The Heidelberg man, moreover, appears to have been the precurser, perhaps

Courtesy, American Museum of Natural History

FIG. 327. THE EVOLUTION OF THE LANCE POINT THROUGH THE SEVERAL STAGES OF THE OLD STONE AGE.

the actual progenitor, of a race which was later to show pronounced signs of progress. This was the great Neanderthal race, and because of his possible ancestral relation to it, Heidelberg man is often spoken of as Pre-Neanderthaloid.

The actual advances made by Paleoanthropus are difficult to trace in those relics indicating his powers in handicraft. He probably was a most capable hunter and fairly effectual in protecting himself from his natural enemies. That he never reached a high stage of intelligence is evident. In the long period of his existence he may have been slowly evolving until at length it was possible for him to give rise to a more intellectually able race which has left a remarkable record.

Piltdown Man. While this slow human advance was taking place, there came into western Europe another race of Pre-Chellean men, some time probably in the First Interglacial Period. This species of mankind is known as *Eoanthropus*, the dawn man of Piltdown, whose antiquity is placed by most authorities at one hundred thousand and more recently (Osborn) at one million years ago. It is probable that he was contemporaneous with the Heidelberg man, living along with him for a great period of time, perhaps often sharing with him many of the characteristics of his industry and culture.

There are good reasons to believe that the industries both of Eoanthropus, the Piltdown man, and of the Pre-Neanderthaloid Heidelberg race became Pre-Chellean in their ultimate period. Both of these races made use of chance and accidental forms of flint and stone, retouching them to a limited extent in such a manner as to give point to the tool or else to fashion a crude rasping surface. One of the most important of these prehistoric implements, the so-called *coup de poign*, or hand-ax, was developed during these Pre-Chellean times. Additions to the list of the Pre-Chellean equipment for industrial and domestic purposes were the knife (couteau), the hammer stone (percuteur) and perhaps the throwing stone (pierre de jet). In their very primitiveness these instruments reveal the first experimental stages in the development of implements.

The dawn man of Piltdown, like his Heidelberg contemporary, was still a nomad. He wandered from station to station, pursuing the track of the great game upon which he depended for his food. He lived near the course of the great rivers, showing no tendency toward the establishment of permanent abode. He was a restless migrant following the dictates of the seasons almost as instinctively as did the migratory birds and beasts. As yet he had not learned those secrets which later enabled him to stand against the vicissitudes

FIG. 328. MANUFACTURING FLINTS, THE RIGHT HAND CLIPPING, THE LEFT HAND HOLDING, ILLUSTRATING AN IMPORTANT INFLUENCE IN THE DEVELOPMENT OF RIGHT HANDEDNESS.

of climate. His acquisitive proclivities were still in the crude. The idea which gave him the self-assurance to stake out his claim, to assert an inalienable right to his own angle of earth was also in embryonic state. Indeed, the foundations of that possessive sense destined to become one of the chief characteristics of the human race, to be at length the ruling passion of humanity, had only been laid down in their most simple instinctive rudiments.

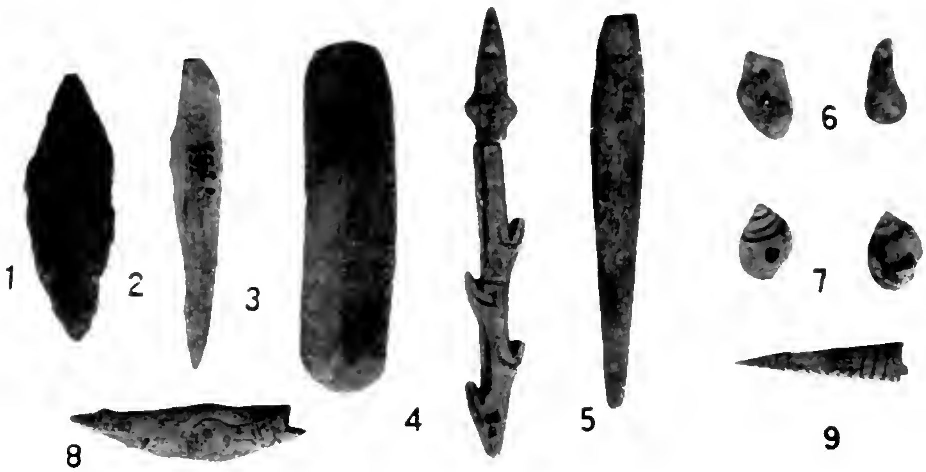
Chellean and Acheulean Stages. The next or *Chellean Period* had an active development which adapted it to the roving lives of the bold hunters who lived in the open and whose entire industry was produced in response to the needs of the chase. As the Pre-Chellean period drew to its close early in the Second Interglacial, evidences of another race became apparent in western Europe. This new arrival was the *Neanderthal man* or *Homo pri-*

FIG. 329. MANUFACTURING FLINTS, THE RIGHT HAND CLIPPING, THE LEFT HOLDING, ILLUSTRATING AN IMPORTANT INFLUENCE IN THE DEVELOPMENT OF RIGHT HANDEDNESS.

migenius. His race in its first rapid development passed through a cultural phase somewhat in advance of the Heidelberg, for his progress is shown by a great increase and a considerable refinement in the small instruments formerly employed. Such improvement particularly affected the *coup de poign* which, in addition to its many and varied forms, was now equipped with a sharp cutting blade in the manner of a chisel or adz-like tool for fashioning wooden implements. The flint instruments of the next stage belong to what is recognized as the *Acheulean Period*. Flint points to form darts and spearheads were then added to the equipment of the chase.

Mousterian Stage. It was not, however, until some time during the fourth glaciation (about 150,000 years ago) that the Neanderthal race, passing through its remarkable *Mousterian* cultural phase, took a decisive step forward, at once so critical, so epoch-making that the importance of its far-reaching psychological effects has scarcely as yet been fully appreciated. This profitable step—and it may well be called such—has made itself felt with increasing force upon all the subsequent development of the human race. It actually led the Neanderthal man to the threshold of a new idea. The ultimate expansion of this new idea was to become one of the keystones of all social organization, if not the fundamental principle in the upbuilding of human society. This great step forward gave the Mousterian the first real conception of property holding. It implanted in his mind that germ out of which grew the rights of possession handed down by him as an heirloom to all the remainder of his race and to other races of mankind.

Development of the Conception of Property Holding. The physical basis of the conception of property holding developed from the fact that the Mousterian Neanderthal became a cave-dweller. He sought shelter from the elements in the rude dwellings fashioned by nature. Why he had not seen the advantages of such protection long before this late period in his progress seems quite remarkable, and yet the explanation may not be far to seek. Those caves which he might have found to his liking or suited to his convenience were already inhabited by such dangerous tenants as the cave-lion and leopard, the hyena, the wolf, the great cave-bear, and perhaps even the dread *machaerodus* or saber-toothed tiger. All of these were his natural enemies—for the most part successful ones—with whom he could only at the expense of greatest risk dispute the right of way, to say nothing of the right of possession. Through all the long periods of his upward progress, he had not yet learned the means nor had his hands fashioned the implements by which he could contend with these beasts of prey on anything like an equal footing. They took from him at will and his retaliation was both feeble and ineffectual. They, rather than he, were still the masters of the situation. This condition of affairs was destined to continue until some critical discovery,



Courtesy, American Museum of Natural History

FIG. 330. IMPLEMENTS AND ORNAMENTS TYPICAL OF UPPER PALEOLITHIC AGE.
1. Knife Blade or Spear-point of Flint. 2. Knife or Etching Tool of Flint. 3. Planing Tool of Flint. 4. Harpoon Point of Bone. 5. Lance Point of Bone. 6. Pendants of Elk Teeth. 7. Beads of Shell. 8. Bone Fragment with Partially Etched Horse. 9. Bone Fragment with Traces of Geometric Design.

some happy chance revealed a new instrument or a new method whose deadliness at length placed in human hands the means which gave man his ultimate supremacy over these creatures who had so long terrorized and preyed upon him. That this new agent was the work of his hands can scarcely be questioned. Some modification of the old flint weapons or the shaping of an implement capable of destroying the marauders provided man with such a margin of safety that he no longer came off second best in his contact with his unrelenting assailants. Whether this new agency was a combination of the use of fire with a more efficient weapon, or some other means, the fact remains that Neanderthal man ultimately drove the hostile carnivores out of the caves. These he coveted for himself and there in time established his own dwelling places. This slow and hazardous undertaking undoubtedly required a hardy courage and an unfaltering persistency.

But even a hard-fought contest of this kind could not fail to have a significant psychological influence in the final outcome. Once he had gained the right of ownership, this preliminary struggle all the more emphasized his sense of possession. It doubtless did much also to stimulate those acquisitive elements in his make-up which laid the foundation of the incentives and desires for conquest. Since Mousterian times, throughout his prehistory and history, man has spent much of his effort and energy in exploiting, in codifying, in legislating statutes to justify and regulate this last new development of his possessive instinct. Out of such rights and laws of possession have grown the influences controlling all of his economic and political organization. Much of his moral code has been built up around these rights. Just as they have afforded the justification for the organization of states and empires, so the right to have and to hold became the governing principle in the life of the individual. They have been the incentive underlying competition and success, the motive of pillage and plunder, the inducement for the aggressions of peace and war. In a word, while this expanded sense of possession has become the essential element in all the achievements of mankind, it is no less the instigator of much of the woe and maladjustment in the race.

The Communal Life of Mousterian Neanderthal Man. The Neanderthal of Mousterian times appears to have lived in communities. Such communal life had its effects upon social organization, upon the development of language, upon the expansion of imagination leading to the establishment of tradition as well as to tribal rivalry and individual competition. The self-assertiveness which must have resulted from the realization on the part of man that he had finally gained the upper hand in many details over the natural world caused him to change his attitude from that of a fugitive to that of a conqueror. It was doubtless from this positive self-feeling that there arose most of his more expansive ideas whose multiplication easily led on into the realm of fancy and brought him many illusional interpretations concerning the workings of nature. They also stimulated the beginnings of religious belief and gave him his first incentives for the establishment of customs which manifested themselves in such complex ceremonial rites as those connected with burial and perhaps with sacrifice.

In their remarkably exhaustive studies concerning the mentality of anthropoids, both Professor Thorndike and Professor Yerkes were struck by the great length of time which is necessary for one of these animals to grasp a new idea. The apes in their capacity to learn seem vastly inferior to men, although the learning process appears to be essentially similar. There can be no possible dispute concerning this contrast as between modern man and even the highest apes. But in the retrospect, does it not seem clear that primitive man, in his slow evolving, required an astoundingly long time to grasp a single new idea—great periods of geological time, for example, to learn how to protect himself from the wild beasts or to sharpen his flint implements? Indeed, are not his modern successors in a general way living up to this reputation for the slow acquisition of really new ideas?

Implements of Mousterian Neanderthal Man. Mousterian industry in flint, however different it may have been in its outward expression, still had all the appearance of a direct evolution from Acheulean culture. In some instances there is a distinct improvement over the ideas of the older culture, but again a decline or even suppression in some of its most effective instruments. The same ideas appear to be at work upon the same materials. Mousterian aims, however, were considerably modified by the new mode of living, by the lessened physical resistance which a better sheltered life would afford. The making of clothing undoubtedly grew out of the conditions of this more protected type of life which produced a people less inured to the elements than the hardy races which lived in the open. The effects of this need for clothing made themselves felt not only in industry, but also in the production of implements necessary to such industry. The crowding incident to the sheltered dwelling in the grottoes and caves also had its deleterious influences upon the physical well-being of the Mousterians. Undoubtedly the ravages of infection and contagion became much more potent, and disease as well as imperfect hygiene had opportunity to go their full length in producing inroads upon this race.

End of the Lower Paleolithic Period. Little was added to instrumental perfection during the Mousterian period of culture. The *coup de poign* or hand-ax, so valuable an instrument in earlier cultural periods, had fallen somewhat into decadence, although the chopper, the planing tool, the drill or borer, the knife and scraper were still retained. This last especially had adapted itself to the new needs of their social conditions for it appears in many forms, with a curved edge, a saw edge, a double edge, a beaked edge, or having numerous edges. The hand-stone and the hammer-stone were still in their former Acheulean state, all of these being adapted to industrial purposes. No distinctly new ideas in the implements of war and chase have yet made their appearance, the spearhead, the throwing stone and the knife still being the chief weapons employed during this period.

Whatever insidious influences might have been at work, in course of time the Mousterian culture began to show signs of a steady deterioration. The predominance which the Neanderthal had exhibited as a race in Lower Paleolithic times was distinctly on the wane as this period approached its end.

The Upper Paleolithic and Cro-Magnon Man. A profound change finally appears to have come over the character of the inhabitants of western Europe. For some reason the Neanderthal race disappeared to be replaced by another race of man, the Cro-Magnon. This, without question, was the replacement of a lower race by one of much higher organization. The Neanderthal was distinctly on a lower plane than any now existing human type, while the Cro-Magnon ranks high among the races of mankind in intellectual development and known capacities of production. He belongs to the species Homo sapiens, the same species of man that has made modern history. He was dominant throughout the Upper Paleolithic and passed through many interesting phases of cultural development, characterized, to be sure, by the development of stone instruments, making him, therefore, still a man of the Old Stone Age. But he too, like the Mousterian Neanderthal, ultimately began to decline until his place was finally usurped by the newcomers who more probably were the direct ancestors of the modern European. The advent of the Cro-Magnon into western Europe is usually assigned to the end of the fourth glaciation or the beginning of post-glacial time. The duration of this period, as estimated by most authorities, is placed between 25,000 and 30,000 years. It may, in this light, be concluded that Homo sapiens has been an inhabitant of the European continent for about 30,000 years.

The Cro-Magnon race, like its predecessors in Lower Paleolithic times, had its own well-defined cultural periods. Industrial development expressed itself in innovations, perfections and improvements in the flint instruments previously employed in earlier periods.

The Cro-Magnon as Conqueror of the Neanderthal Man. Professor Osborn, who has carefully assembled and analyzed the evidence concerning the Cro-Magnon invasion of Europe, gives a most illuminating picture of the events which must have transpired in the replacement of the old Neanderthal race by these Cro-Magnon newcomers. Those who would have the details in full are referred to Professor Osborn's chapter on The Main Features of the Upper Paleolithic in his "Men of the Old Stone Age." In substance, the evidence seems to show that the Cro-Magnons brought with them a type of industry which is technically known as *Aurignacian.* At this time the Neanderthals, still in the possession of their country, were practising their waning Mousterian industries. The two types of cultural activity, therefore, came in contact as these two races met, and consequently show the influence of some intermixture. It should be observed, however, that this intermixture was strictly confined to the industries themselves and did not involve either of the two races of man. Even in their burial customs the Cro-Magnons followed the ceremonies of the Neanderthals, choosing the same kind of burial site, interring the dead with implements of industry and warfare.

The result of the encounter between Neanderthal and Cro-Magnon was that of a superior people with a much inferior one. Probably possessed of the bow and arrow, with other advantages for warfare, the Cro-Magnon had little difficulty in the conquest of a people already reduced in physical resistance both by disease and the severe climatic conditions of the Fourth Glacial Period (beginning 70,000 years ago). This dispossession of the Mousterian must have been complete, for in the Cro-Magnon race there is no sign of such admixture as often occurs when a victorious nation, having completely annihilated all of its male opponents, still retained many of the women in the households of the conquering warriors. Men and women alike appear to have shared this extermination of the Neanderthal race. It was probably the increased brain power of the Cro-Magnon which caused this great change to sweep over western Europe at the beginning of post-glacial times. This view is based on the appearance of a large brain case of this race and the development of an almost modern forehead and forebrain.

Cro-Magnon Periods of Art and Industry. The Cro-Magnons were a race which developed in Asia but seem to have had no connection of an ancestral kind with the Neanderthals. They possessed a brain capable of more complex ideas, greater comprehension, more reasoning powers, a wider, more facile imagination. Above all, they were endowed with a highly artistic sense which had not been present in any of the previous races of man. Indeed, they seem to have possessed a cerebral capacity which was nearly if not quite equal to that of modern man. They were capable of advanced education and had strongly developed esthetic as well as religious feelings. Their society was highly differentiated along the lines of capacity and talent for work. Their artistic productions as shown in the mural decorations in their caves were of such excellence as to place them among the truly great achievements of the human kind. The Aurignacian culture established by the advent of the Cro-Magnon race in southwestern Europe ultimately succeeded the Mousterian industry. It introduced the art of engraving and sculpture, together with a greater refinement in all of the instruments employed during the previous cultural periods.

A comparison of the Aurignacian period with the stages which had gone before emphasizes one striking fact. In the pursuits of industry and domestic life, little in the way of innovation was added by the Cro-Magnon race. It adapted and perfected what the Mousterians had used with greater or less advantage. But what it did add, neither the Mousterian nor any other preceding period possessed, namely, tools and implements for sculpture and engraving. Chief among these were the drill, engraver, etcher, carving chisel, mortar, hammer-stone and polisher, all of which were intimately connected with the artistic activities of this new and highly intellectual race of man. The Cro-Magnon also passed through certain cultural phases which show the same general tendencies observed in previous races. As in the first flush of any renaissance, so with the awakening of a new race, the initial period is usually the most fertile in productive ingenuity. Then comes the gradual culmination as it did in the *Solutrean Period* which was the acme of achievement in the flint industry. Declining greatness followed next in the *Magdalenian Age* which brought the closing stage of Cro-Magnon culture. The same familiar cycle of juvenescence, maturity and decline which characterized the development of earlier races did not fail to apply its inevitable formula to the Cro-Magnon. For just as Neanderthal and Pre-Neanderthaloid man passed through successive periods of culture which began with the primitive Pre-Chellean, advanced to the Acheulean, reached its climax and began to decline in Mousterian, so the Cro-Magnon saw the beginnings of his ascendancy in the Aurignacian period when he first introduced the art of engraving, drawing and sculpturing animal forms. His culture and industry were still dictated by a life devoted to the chase and conditioned by such protection as might be afforded by grottoes and similar natural shelters.

Cro-Magnon Industry, Its Rise and Decline. In the next succeeding period the Cro-Magnon reached the zenith of his industrial supremacy. The Solutrean was the high noon of his cultural achievement just as the Middle Mousterian was for the Neanderthal. In this era the flint industry attained its culminating stage but its flourishing activities soon began to wane. Through the Magdalenian all of the artistic and industrial development sank slowly toward the horizon of its disappearance. At length in the *Azilian Period* the last survivors of the greatest race in the Old Stone Age, senescent in their industries, decadent in their art, saw the setting of the Cro-Magnon sun and the passing of their kind into the darkness.

Characteristics of Cro-Magnon Art. Many vicissitudes beset the Cro-Magnon industries due to influences of trade invasions and new inventions. But in their art they revealed one continuous evolution and sustained development. An impressive feature about Aurignacian art is the fact that it seems to have escaped that period of infantilism which is almost universally observed in the artistic development of primitive races. The Cro-Magnon first manifests his artistic effort in a period of virile youth. His art passed directly into a stage of relative maturity based upon his keen appreciations of the animate world with which he was in constant contact. The Aurignacians possessed a true sense of proportion and of beauty which appears to have been theirs as if by instinct. The treasures of their art galleries upon the walls of the ancient caves, their remarkable drawings, sculptures and paintings fully warrant the distinction which has been conferred upon them in the title of *Paleolithic Greeks*.

The paleolithic artist resembled both the Greeks and the Egyptians in that he was not content with plain, uncolored sculpture. Like them, he had recourse to painting his reliefs whether they were of the bison, the horse, the deer or the great mammoths. It was his wont to color such sculptures with a violet tint, which may have been a compound of manganese, or with a red ochre as well as certain other pigments concerning whose use he already seemed familiar. What characterized the Cro-Magnon's art more than all else were his close powers of observation and his accuracy of reproducing what he saw in the animal forms which he chose to depict. The relative simplicity of his technical execution depended upon the employment of the fewest possible lines and the boldest of strokes; these suggested more than they portrayed. It was this very simplicity which gave his art its appearance of maturity from the first. It enabled him to express his esthetic feelings with more telling effect than if he had depended upon an infinite amount of detail. To this accuracy of observation and simplicity of execution he imparted a third great quality which makes his art live in a class well up to the standards of later and higher periods of artistic development. This third element was the sense of motion and activity, particularly of locomotion, with which he endowed the animals carved upon the walls of his caverns, upon bone or ivory, or merely drawn in simplest outline. Perhaps it is safe to say that few, even with all of the refinements of technical procedure, have surpassed him in that infusion of vitality which signalizes his art.

Reasons for the Development of Aurignacian Art. Although it is clear that even before the appearance of the Cro-Magnon race the much simpler Mousterian man had shown the first tendency toward permanency of abode and the establishment of property rights, it is nevertheless true that even these Upper Paleolithic men for the most part were still nomadic hunters. Why, then, did they in the dark recesses of their caverns resort to these artistic activities? What incentives led them to their carving upon bone and ivory? These could scarcely be the meaningless diversions which helped to pass unoccupied hours when not engaged in hunt or combat. Their artistic efforts and productions assuredly had some more serious and pertinent object in their lives than this.

Many hypotheses have been advanced to explain this remarkable outburst of artistic enthusiasm and devotion in these early times. One view holds that the cavernous art galleries were the schools which contained the models of artistic productions, the copies of which were much desired by many members of the race. The caves, therefore, where these mural decorations were made, served as the workshops of copyists who would reproduce in bone or stone facsimiles of the actual artistic performances of the Cro-Magnon artists. Such reproductions gave a wider distribution to their art among the scattered communities. This view, however, has but little to recommend its acceptance. It seems probable that some much more telling motive incited the arduous efforts which the artistic mural productions demanded. In the history of primitive races whose records are available for study, it has repeatedly occurred that drawing and design have a special significance with reference to the actual maintenance of life. The Australians, for example, draw upon the ground pictures of the animals they use for food. Sitting in a squatting position about these pictures, they perform certain incantations which they believe will insure a plentiful supply of what they need. The American Indians are in the habit of carving images of animals and also of drawing designs representing rain. In the presence of these emblems they perform religious ceremonies and devoutly believe that they may thus secure abundant harvests and success in their hunting expeditions. Images and pictures are essential features in these propitiatory ceremonies, a sort of magic talisman by means of which to exercise an influence over those animals which serve for food.

It is not necessary, however, to pass so far back as the prehistory of the Old Stone Age, or even to investigate the superstitions of people still remaining in the most primitive stage of ethnical advancement, to detect the working of this superstition. It was not so long ago that the picture of a man was believed to be an actual emanation from him and that the possessor of such a picture must exert power over the person whose presence might thus mysteriously be conjured up. Only a few centuries ago this was a common belief, and many learned judges condemned both men and women to death on the evidence of their having possessed images or pictures of people they were accused of bewitching. It is not at all unlikely that there are still to be found to-day in Naples or Sicily certain sorcerers who, for a stipulated price, will undertake to destroy any undesirable individual by the relatively simple executionary method of sticking pins into the wax image of the person thus proscribed, or by melting the image before a slow fire. In this light it may be understood why the Australian natives and American Indians set such store by the pictorial representation of those elements in nature which contribute to their stock of foodstuffs. It is also to be noted that the Aurignacian and in fact all of the Cro-Magnon art tends to portray those forms of animals which were employed for food, while those animals not so employed are conspicuous by their absence from these artistic reproductions. While this may not be accepted as the final solution of that question — why did Paleolithic man resort to art? — it may nevertheless offer a working hypothesis to show an essential ulterior motive for his efforts in this direction. To his mind at least his works of art assured him peculiar magic control over the animal life which was necessary to his maintenance and well-being.

Man's Progress Following the Decline of the Cro-Magnon Race

Cro-Magnon destiny was no exception to what had gone before or what would follow many times thereafter. It embraced the irresistible tendency toward racial decline with final extinction, and this was the fate which did at length befall Cro-Magnon man. As the day of his ascendancy waned, a new race invaded western Europe. Thus the Old Stone Age came to its conclusion approximately 10,000 years ago, with the advent of the more vigorous Neolithic man. He developed an innovation in the construction of his implements in the fact that he now polished the stone. The principal change, however, was an economic one, namely, the introduction of a rudimentary knowledge of agriculture with the corresponding use of a variety of plants and seeds. This naturally was accompanied by a gradual development of tools and implements for the preparation of the soil and the garnering of the harvest. As tiller of the soil or as herdsman, there was equal need for a permanent abode. What, therefore, in earlier Mousterian times gave the first decisive impulse to the upbuilding of the possessive sense, now found still more substantial inducements to incite the acquisitive tendencies of man. At this time also pottery was introduced and used in the preparation of food. These two great changes affecting the food supply of the race had far-reaching effects upon the actual metabolism of the people. Cultivated crops of various kinds now gave a greater variety in carbohydrate nutrition, while cooking produced modifications in the proteins which must have had their effects upon the processes of digestion. The advantages of domesticating many animals for food supply were realized early in Neolithic times. Domestication also brought to man's aid the services of the horse in transportation and conveyance. Two varieties of cattle were successfully domesticated, the Celtic shorthorn and the longhorn. In fact, the New Stone Age witnessed a domestication of animals which corresponded closely with that of present times and included cattle, sheep, goats, pigs, horses and dogs.

Before the close of Neolithic time all of the direct ancestors of the modern European races had established themselves in western Europe. With the advent of the Bronze Age, man was rapidly attaining those manual capacities whereby he might transcribe a record of himself, and thus enter upon an epoch of real historic consciousness. Some authorities set the beginning of this historical period only as far back as the commencement of the Egyptian calendar between four and five thousand years ago. This dawn of history was followed by a procession of great events beginning in the early pre-dynastic eras of Egyptian civilization. The subsequent developments of the Pharaonic art and culture, the successive resplendence of Chaldean, of Babylonian, of Grecian and of Roman achievements in the realms of civil, artistic and philosophical organization need little further comment than to note in what great measure all of the remarkable progress was the work of the human hand. Each civilization in its turn contributed to the development of the race which, passing through the long eclipse of the dark ages of medieval times, emerged again in the brilliant light of the Renaissance and has gone forward with a steady progress in material accomplishments into modern times.

The Birthplace and Migratory Trails of Mankind

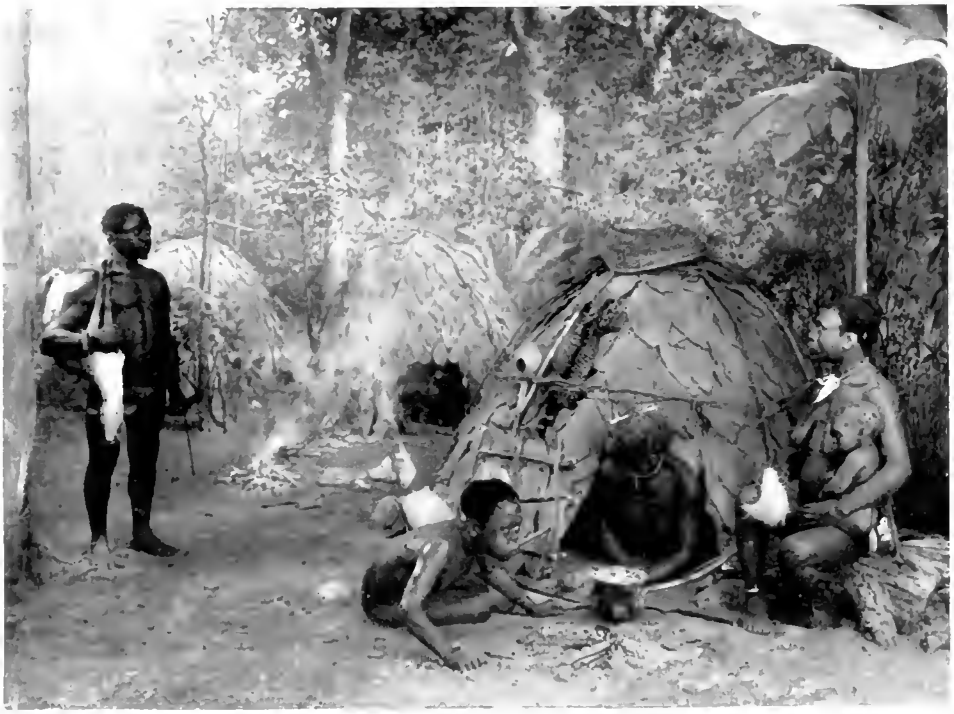
The cradling place of mankind has been a matter of much speculation. It is now generally accepted that this was located not in Europe, but rather in the extensive central regions of the Asian continent. From such a birthplace the race has gone forth in successive waves of migration to the north, to the east, to the south and to the west. These successive waves have not brought forth a uniform product, nor have the results of the development of the people thus migrating manifested the same ethnological progress or specialized differentiation. Indeed, there seem to be certain almost irresistible influences at work in consequence of the course and direction which the various migrations have taken.

Courtesy, American Museum of Natural History

FIG. 331. AUSTRALIAN NATIVE.

The Australians resemble the negro and negroid populations in the dark chocolate brown color of the skin. They have hair which is wavy but never wooly. Average height is 5 ft. 5 in.

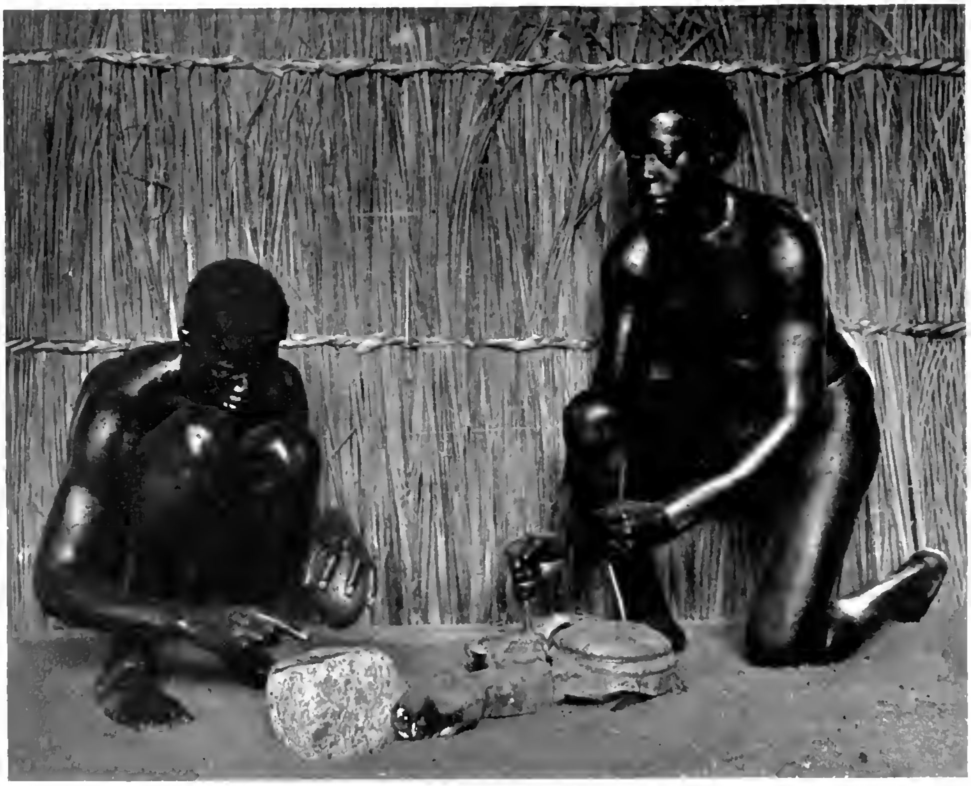
The Westward Route. Of all the migratory routes, the westward passageway alone proved to be the path of progress. Those who have pursued this course inevitably came under the spell of stimulating forces which



Courtesy, American Museum of Natural History

FIG. 332. AN AFRICAN PYGMY GROUP FROM THE BELGIAN CONGO.

seemed to shape their development as if by some long-predestined formula. The westward trail led to slow but steady rise in specialization with intellectual and cultural advancement as its first phase. The second stage was one of culmination in which all of the activities of the mind and body reached their highest point. Then came the third stage characterized by a progressive decline with every evidence of decadence in industry, art and manners. At length in the last phase, as if at the instigation of some pursuing Nemesis, there came a gradual reduction and final disappearance of the race. So it has been with every wave of migration which has come from Asia into Europe, lured on by the westward trail, seeking the advantages of the great Mediterranean basin, in some instances pushing onward to the west even as far as the seaboard of the Atlantic.



Courtesy, American Museum of Natural History

FIG. 333. THE AFRICAN NEGRO.

THE SOUTHERN ROUTE. Something in the migratory passage to the west, something in the country which it laid open to the newcomers stimulated them to progress as no other part of the world has done. The southward trail leading into Africa had no such successful influence on the invaders who infiltrated its terrain. Those who migrated to the south were shut off from the beneficial contacts and competition with progressive peoples and so have remained in the condition of primitive races. The southeasterly trail, likewise, afforded but little stimulus to advance beyond the earliest stages of human development. The inhibitory effects of migration to the south and southeast upon racial evolution are clearly visible in many native tribes inhabiting these parts of the earth. In certain localities some of the representatives of modern man have scarcely attained the plane of Chellean culture. Their ethnological phase of development may rightly be considered as Pre-Paleolithic. This is true, according to Obermaier, of the pygmies of Central Africa, the Semangs and Senci of Malacca, the Negritos of the Philippines, the Kubus of Sumatra, the Asiatic Pygmy tribes and the Andaman Islanders. These last employ only wood, bone and shells in their industry; they have not even acquired the use of fire.

THE EASTERN ROUTE. The eastern trail, leading as it originally did by land connection into North America, although it took the American Indian to his famous hunting grounds and put in his possession a land of unsurpassed fertility, none the less restricted him for all the period of his history and prehistory to the exercise of a nomadic life. Approached from this direction, North America offered no further advantages to mankind than did either of the other routes of migration. The real fertility and productiveness of this continent appear to have required a previous period of European experience in order that its actual richness might be developed and materialized.

THE NORTHERN ROUTE. The northern trail led the Eskimo to his Arctic isolation where he found an environment barely habitable and thoroughly unproductive in its contributions to human progress. All of these trails alike, the southerly, the southeasterly, the easterly and the northern, have proved to be paths of inhibition. Offshoots of the race which have pursued these routes invariably manifest their retardation by the retention of many primitive characteristics through all the generations of their existence. Some of them have passed through successive stages of industrial and cul-

FIG. 334. THE AMERICAN INDIAN.

tural activity not unlike those of the Old Stone Age. It is remarkable, however, that the westward trail alone was the road to progress. It was the trail which led to all the great events of human history. It has taken man through

FIG. 335. THE ESKIMO.

his long prehistoric era of progressive achievement and through the briefer space of his brilliant historical record.

THE DRAWBACKS OF THE WESTERN ROUTE. And yet the western route was not without its drawbacks. Whatever glories might come of following it were temporary at best. Man moved along its course in an unfailing cycle, which had a metrical rhythm almost as exact and quite as foreboding as the chorus of the ancient Greek tragedy. There was that phase which announced his arrival or awakening, that rise which gave the full measure of his worth, that slow but sure decline, that invariable destruction which overtook him. The persistent procession of these phases seemed to exert a baneful influence on all his efforts toward progress, whether the part he played was that of

Courtesy, American Museum of Natural History

FIG. 336. A GROUP OF BRITISH SCIENTISTS DISCUSSING THE PILTDOWN SKULL.
STANDING, LEFT TO RIGHT: Mr. F. O. Barlow, Prof. Elliot Smith, Mr. Charles Dawson, Dr. A. Smith Woodward.
SITTING, LEFT TO RIGHT: Prof. A. S. Underwood, Sir Arthur Keith, Mr. W. P. Pycraft, Sir E. Ray Lancaster.

Heidelberg or Piltdown Man, Neanderthal or Cro-Magnon, Egyptian or Babylonian, Greek or Roman.

ADVANTAGES COMMON TO THE MEDITERRANEAN AND EUROPEAN TERRAIN. What have been the advantages in the Mediterranean and European terrain not common to other territories of the earth? Perhaps some conditions of immunity, some subtle dietary influences upon the endocrine system, some bacterial or parasitic symbiosis peculiar to the temperate zone gave man greater psychic zest and more physical vigor than his less energetic brothers of the tropics. It may have been an increased fecundity, a greater viability of offspring, which assured rapidly multiplying populations, keener rivalry and quickened intelligence. Nor should the possibilities of mutations in cutaneous melanism be overlooked. The lack of black pigment in the skin makes tropical existence difficult for white races and thus enforces a northern habitat. These problems of ecology and mutation may well deserve most extended investigation, not alone to disclose the causes active in producing the remarkable progress of European races, but, if possible, to determine what factors have consistently contributed to their decline. It is not improbable that the tendency toward degeneration, so notable in European history, has a purely sociogenetic explanation. Oligarchical concentration of political control inevitably spreads the contaminating effects of luxurious living and relaxation from effort to the multitude so governed. Professor Osborn insists that mankind in his uncivilized state is subject to the same orderly laws as those which prevail throughout the animal kingdom, but the introduction of civilization interferes with the natural regulation of things and man himself appears to be upsetting the order of human progress.

The Great Factor in Human Evolution

From first to last, it has been the achievements of his hands which have carried man onward from the time when he began to work with the simplest of stone implements. Some authorities maintain that it was the development of the brain which led to the attainments distinguishing man from other animals. Some attribute the distinction to his assumption of the erect posture. Still others ascribe all of human progress to the development of speech. Unquestionably, each of these factors is inseparably associated with human evolution. But if one among them were to be selected as the most potent developmental incentive, first choice would seem to fall most naturally to the specialized structure of the body best adapted to externalize the neural energies of the brain. Such a flexible instrument as the human hand seems preeminently fitted for these purposes. With the brain to direct its action, to expand its usefulness, the upright posture to give freer range to its execution, with speech to make its accomplishments communal, to introduce the benefits of cooperation, the hand became the master key opening all of the ways leading through the new and vast domain of human behavior.

Chapter XXV

THE BRAIN OF MODERN MAN

Weight and Indices of the Human Brain

THE weight of the human brain in the full-grown adult is between 1100 and 1500 gm. In the large proportion of cases the male brain weighs between 1304 and 1502 gm., the female brain, 1134 and 1332 gm. In man the brain seems to show some fluctuation in weight dependent upon the age of the individual. Its greatest weight according to the time of life is found in the middle decades, from thirty to fifty years. Before this time the weight gradually increases until it reaches its middle-age maximum and thereafter decreases, losing progressively as old age advances. Statistics indicate that the brain weight of distinguished and talented individual members of the race is somewhat in excess of the average adult brain. Thus, in one hundred distinguished men, the average weight of the brain was [illegible] gm., about 100 gms. above the average weight of European brains. The usual senile decrease in weight is apparently delayed about ten years in those considered distinguished. The brain weight in different races of man shows some slight differences. Thus, the average Chinese brain weighs 1330 gm., that of the Sandwich Islander about 1300 gm., the brain of the Malay and the American Indian, 1265 gm., the brain of the African Negro, 1245 gm., the brain of the native Australian, 1185 gm., the brain of the [illegible] 1100 gm. The weight of the Latin brain is somewhat less than that of the Teutonic and Slavonic races.

The following tabulation is based on estimates of the capacity of the cranial cavity in the prehistoric races of man:

Trinil race (Pithecanthropus erectus)	[illegible]
Piltdown race (Eoanthropus)	[illegible]

Neanderthal (Homo primigenius) . . . . 1626 c.c.
Grimaldi race . . . . 1580 c.c.
Cro-Magnon race . . . . 1590 c.c.

The encephalic indices, calculated both by weight and volume of water displacement of the human brain in a series of adult males and females, give the following figures:

Forebrain index . . . . 86 to 89 per cent
Midbrain index . . . . 1 to 1½ per cent
Hindbrain index . . . . 9½ to 13 per cent

These indices of the encephalon place the human brain at the head of that class characterized by pronounced manual differentiation.

Surface Appearance of the Brain in Man

Two facts are impressive upon inspection of the cerebral hemisphere in man when compared with all of the lower primates: first, the marked increase in size; second, the great complexity of convolutional richness and intricacy of fissural pattern. A third feature may be mentioned; namely, the fact that the occipital lobe not only entirely covers the cerebellum but protrudes and actually overhangs it.

THE CEREBRAL HEMISPHERE

The lobation of the human brain seen upon the lateral convexity of the hemisphere is more difficult to discern than in any of the great anthropoids or lower primates. This is due not so much to the fact that the characteristic boundary lines are less prominent, but because of the great complexity of convolutional detail. It becomes more difficult to identify the typical landmarks because they are surrounded by areas which gain so much in detail that their own definition is overshadowed by adjacent features. In another respect this lateral surface differs from that of the great anthropoids and other primates; namely, the almost complete disappearance of the most characteristic of simian fissures, the sulcus simiarum. Thus, the actual boundary between the parietal and occipital lobes is for the most part wanting in man. The occipito-parietal incisure, whose continuation upon the mesial surface is the occipito-parietal fissure, marks the position of this boundary. The extent to which this incisure projects laterally upon the convexity of the hemisphere varies in different individuals and also in the two hemispheres of the same brain. Often it is scarcely apparent beyond the superior longitudinal fissure, or may extend for a distance from 3 to 5 cm. upon the lateral aspect. In no instance, however, does this sulcus have the prominence which the simian fissure presents in the anthropoids.

THE FISSURE OF SYLVIUS. Of the primitive anthropoid fissures, only two may be discerned with certainty upon the lateral surface of the human brain. These are the fissure of Sylvius and the fissure of Rolando. The Rolandic fissure separates the frontal from the parietal lobe. The fissure of Sylvius separates the frontal and the parietal lobes from the temporal lobe. The division between the parieto-temporal area and the occipital region is an indecisive one. These three areas of the brain become confluent in a common meeting-ground. The fissure of Sylvius is the most prominent fissure of the human brain. It forms an angle of something a little more than 45° with the cerebral base line. This portion of it is known as its posterior ramus. Upon the basal surface, between the orbital portion of the frontal lobe and the tip of the temporal lobe, is the horizontal limb of the fissure. On the lateral surface the fissure divides into a short anterior limb, a longer anterior ascending limb and the posterior limb already mentioned. The ascending limb (ramus anterior horizontalis) is about 2 cm. in length; it passes upward and slightly forward into the caudal portion of the inferior frontal convolution. The horizontal branch (ramus posterior) is the main lateral continuation of the fissure. It passes backward and slightly upward for a distance of approximately 8 cm. This part of the fissure forms the boundary between the frontal and parietal lobes above and the temporal lobe below. It usually ends by

FIG. 337A. DORSAL SURFACE OF BRAIN, HOMO SAPIENS.
[Actual Length 156 mm.]

dividing into two short arms, one of which enters the parietal lobe and the other extends downward into the temporal lobe. The three divisions of the Sylvian fissure upon the lateral surface of the hemisphere demarcate certain portions of the inferior frontal, parietal and superior temporal convolutions. The portion of the inferior frontal convolution lying below the anterior horizontal branch forms the *pars orbitalis*, or the orbital operculum; the portion of the convolution between the anterior and ascending branches forms the *pars triangularis*, or intermediate frontal operculum; caudal to the ascending

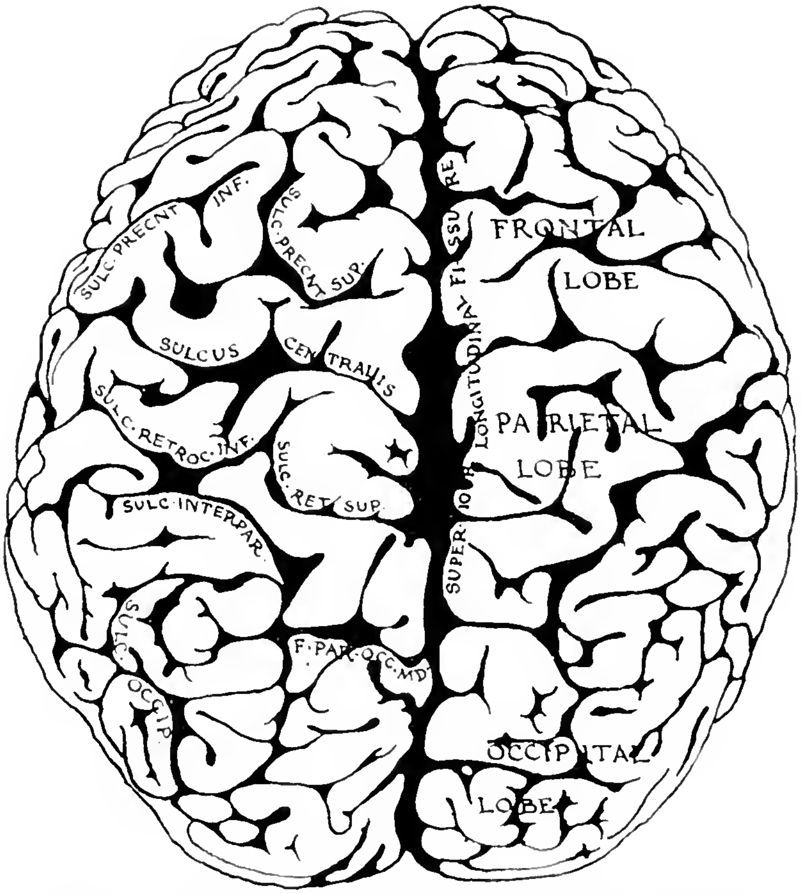


FIG. 337B. DETAILED DIAGRAM OF DORSAL SURFACE OF BRAIN, HOMO SAPIENS. KEY TO DIAGRAM. SULC. INTERPAR., Sulcus Interparietalis; SULC. OCCIP., Sulcus Occipitalis; F. PAR. OCC. MD., Fissura Parieto-occipitalis Medialis; SULC. PRECNT. INF., Sulcus Precentralis Inferior; SULC. PRECNT. SUP., Sulcus Precentralis Superior; SULC. RETROC. INF., Sulcus Retrocentralis Inferior; SULC. RET. SUP., Sulcus Retrocentralis Superior.

branch of the Sylvian fissure is located the *pars basalis*. All of these divisions of the Sylvian fissure and the areas upon the cerebral cortex which are demarcated by them are poorly defined in the great apes. The chief difference between the anthropoids and man in this feature of the brain is the much more marked degree of complexity in the individual components of the Sylvian fissure due to greater intricacy in the convolutions surrounding them. The arrangement of the various subdivisions of the Sylvian sulcus is subject to some variation. For further details in this regard the reader is referred to standard works on the anatomy of the human brain.

THE FISSURE OF ROLANDO. The Rolandic or central fissure of the brain extends obliquely across the lateral surface of the hemisphere in such a way as to interrupt the general longitudinal course of the gyri and sulci of this region. It is bounded by two long oblique convolutions, the precentral and postcentral gyres. The fissure begins near the vertex in relation with the superior longitudinal fissure and often incises the mesial surface of the hemisphere. Its point of origin on the vertex is slightly behind the midpoint of the superior longitudinal fissure, a little further back in man than in the great anthropoids. From this point it passes outward, downward and forward to end near the middle of the fissure of Sylvius whose posterior limb it sometimes, though rarely, joins. At the junction of its upper and middle thirds the fissure of Rolando presents a deep curve with the concavity directed forward. The upper and lower limits of this bend in the fissure constitute the superior and inferior genu respectively. The lower or inferior genu of the fissure extends almost vertically and terminates in close relation with the fissure of Sylvius. The angle of inclination of the central fissure with the mesial plane in the adult brain averages 71.7°. This angle is essentially the same as in the great anthropoids, although in many instances in the lower primates the angle is much nearer 90°. In certain exceptional instances among the great anthropoids this angle varies from 75° to 80°.

THE PARIETO-OCCIPITAL FISSURE. The parieto-occipital fissure is best seen upon the mesial surface and has but slight representation upon the lateral convexity in man. On this surface, as the parietal incisure, it is continued transversely but a short distance, usually on the average of about 12 mm. The line connecting this portion of the fissure and the pre-occipital notch establishes an arbitrary boundary between the occipital lobe behind and the temporal and parietal lobes in front. In all of the anthropoids this external portion of the parieto-occipital fissure is concealed in the sulcus simiarum which intervenes between the parietal and occipital lobes. It is doubtful whether any fissure, even as a vestige, in the human brain may be homologized with the simian sulcus. Some authorities, however, maintain that it is present in the majority of human brains as a curved sulcus, called the sulcus occipitalis lunatus, situated on the lateral aspect of the occipital lobe.

LOBATION OF THE BRAIN. Lobation of the brain is not so clearly defined as in the anthropoids. The boundary line established by the Rolandic fissure separates the parietal from the frontal lobe, while the Sylvian fissure separates the frontal and parietal lobes respectively from the temporal lobe, and the arbitrary line from the parietal portion of the parieto-occipital sulcus to the pre-occipital notch in general is presumed to indicate the anterior limit of the occipital lobe. In all four lobes discernible upon the lateral convexity of the human brain, the most impressive feature is the richness of convolution and of fissural pattern apparent in the frontal lobe. As compared with this corresponding region in all of the great anthropoids and all other primates, the complexity in convolutional design is so striking as to constitute perhaps the chief structural difference between man and the apes. The greater degree of frontal development apparently has moved the superior extremity of the central sulcus further toward the occipital pole. In man a little less than one-half the lateral aspect of the hemisphere is occupied by the frontal convolutions. The highest anthropoid fraction is one-third. By actual planimetric measurement the frontal area in man covers 47 per cent of the entire lateral surface, in chimpanzee 33 per cent, in gorilla 32 per cent, in baboon 31 per cent and in lemur 23 per cent. It is, therefore, in the expansion of the frontal lobe, both in the area covered by it and the great increase in the complexity of its convolutions, that the human brain

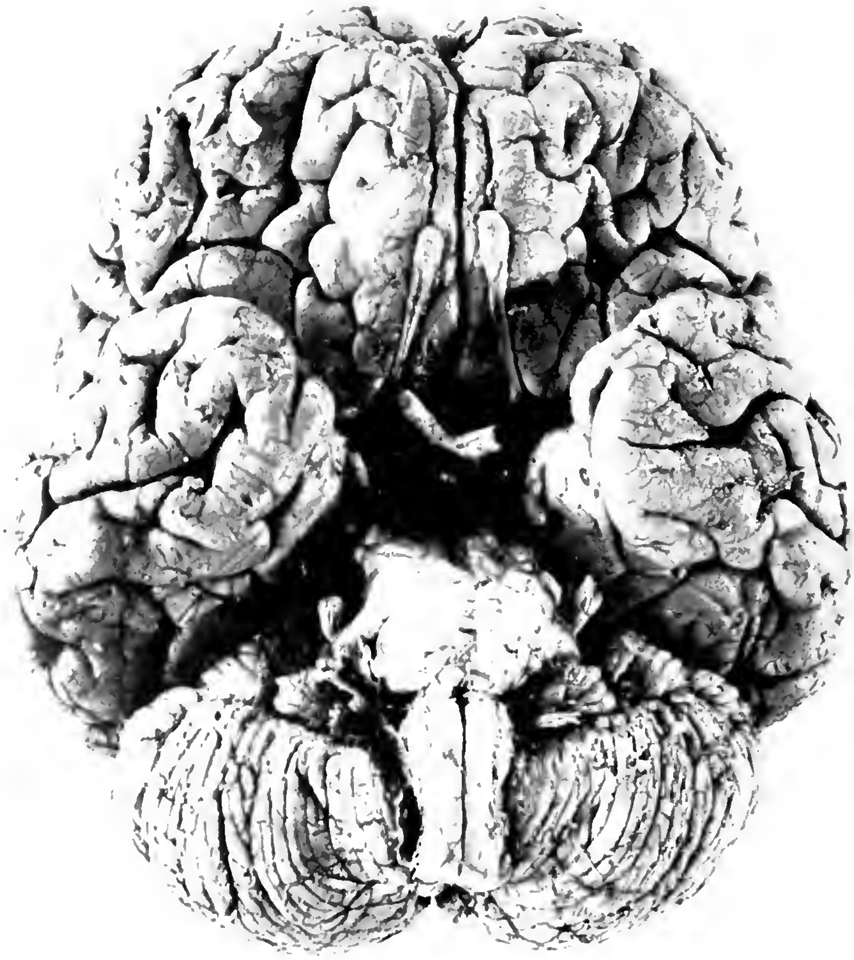


FIG. 338A. BASE OF BRAIN, HOMO SAPIENS.

stands in striking contrast to the anthropoids. The convolutional complexity is likewise increased in the occipital region, and this is also true, perhaps to a less extent, in the temporal and parietal areas. These regions.

which in the lower primates are preeminent because of their rich convolutional pattern, in man seem to be less striking when compared with the frontal and occipital lobes.

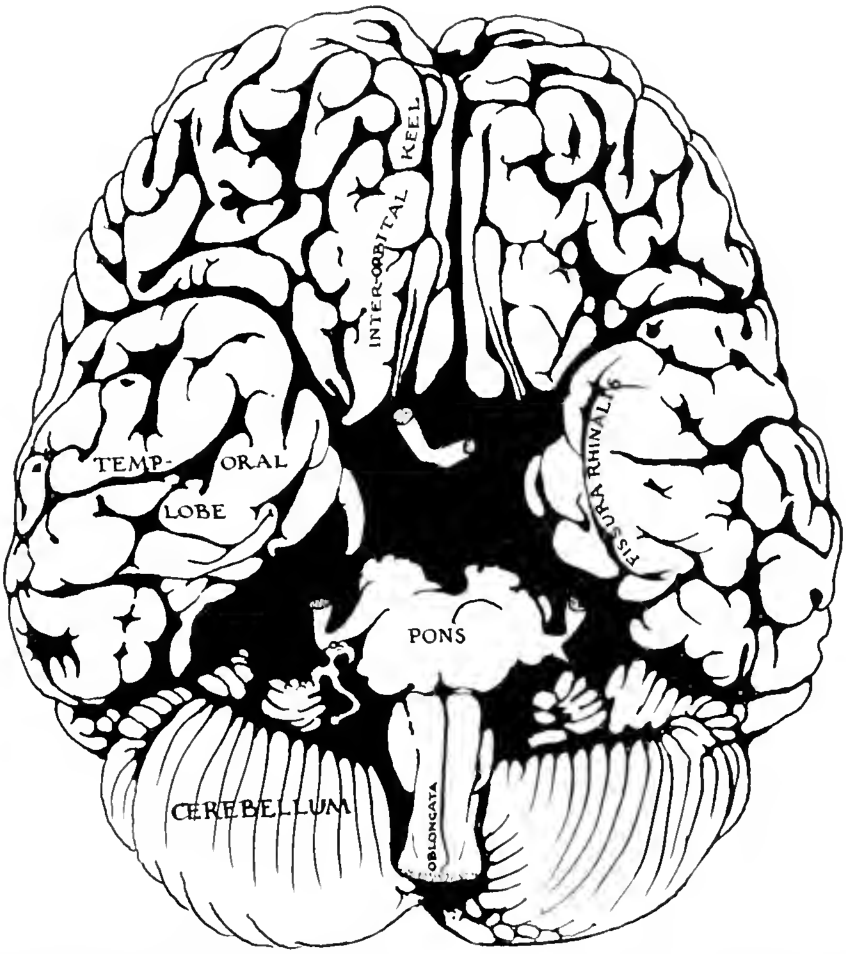


FIG. 338B. DETAILED DIAGRAM OF BASE OF BRAIN, HOMO SAPIENS.

The Frontal Lobe. The lateral surface of the frontal lobe presents a superior, middle and inferior frontal convolution as well as a precentral convolution sometimes spoken of as the ascending frontal convolution. All of these convolutions are exceedingly irregular in outline, and separated from each other by correspondingly tortuous fissures. The superior frontal gyrus is situated between the margin of the hemisphere and the superior frontal sulcus; it corresponds to the upper part of the hemisphere and is much longer than any of the other frontal convolutions upon the lateral surface. It is continued mesially to the marginal gyre on the mesial surface and joins the central convolution by means of a lateral bridge at the upper end of the precentral fissure. The middle frontal gyrus is parallel to the superior frontal convolution in a general way, separated from it by the superior frontal sulcus. The superior and inferior precentral sulci separate this gyre from the central convolution although a well-marked deep annectent gyrus usually connects them. The inferior frontal convolution, the smallest of the three gyres in this region, is in some respects the most important of them all. It is situated in relation with the horizontal and ascending branches of the Sylvian fissure. These branches divide the inferior frontal convolution into three parts, the anterior frontal operculum (pars orbitalis), the intermediate frontal operculum (pars triangularis) and the posterior frontal operculum (pars basalis). The left inferior frontal convolution is often called *Broca's convolution* and it is regarded as the motor speech center. In man it is more developed upon the left side in right-handed individuals. This greater development particularly affects the triangular part of the convolution which may entirely separate the horizontal and ascending branches of the Sylvian fissure.

The Parietal Lobe. The parietal lobe presents an extensive and irregular quadrilateral outline. It is bounded by the Rolandic fissure in front, below by the fissure of Sylvius, and behind by the imaginary line connecting the pre-occipital notch with the external portion of the parieto-occipital fissure. Upon its lateral surface the parietal lobe is divided by an interrupted fissure, the intraparietal sulcus, into three convolutions, the post-central, superior parietal and inferior parietal gyres. The intraparietal sulcus commences at the cephalic angle of the lobe a short distance above the Sylvian fissure with which it is sometimes continuous. It extends for about an inch parallel with the fissure of Rolando and then curves backward and slightly upward, across the parietal surface into the occipital lobe. This sulcus usually appears in three distinct parts which form the superior and inferior postcentral sulci and the horizontal intraparietal fissure. The inferior postcentral sulcus, situated behind and parallel to the lower part of the fissure of Rolando, is separated in about 72 per cent of cases from the superior postcentral sulcus. The superior postcentral sulcus lies behind and parallel with the Rolandic sulcus, dorsal to the horizontal limb of the intraparietal sulcus. The horizontal intraparietal sulcus passes backward and slightly upward. It is often continuous at its cephalic extremity with the postcentral sulcus. The convolutions on the lateral surface of the parietal lobe are three in number, the postcentral, the superior parietal and the inferior parietal, the last being subdivided into certain accessory gyres. The postcentral or ascending parietal convolution constitutes the caudal wall of the Rolandic fissure. It is bounded caudally by the postcentral sulcus in its two subdivisions. The lower extremity of this gyre is connected with the precentral convolution in front and the inferior parietal gyre behind by means of annectent gyres. The superior parietal gyrus is situated caudal to the superior postcentral sulcus, dorsal to the horizontal limb of the intraparietal sulcus. The inferior parietal gyrus is situated between the inferior postcentral sulcus, the Sylvian fissure, and the horizontal limb of the intraparietal fissure. This convolution is more complex in its configuration than either of the preceding gyres. It is subdivided by the upturned end of the Sylvian fissure, also by the caudal termination of the first and second temporal sulci. The extremities of these fissures determine the position of the supramarginal and angular gyres. The supramarginal gyrus passes around the upturned end of the Sylvian fissure; the angular gyrus bears a similar relation to the upturned end of the superior temporal sulcus, and the postparietal gyrus curves about the extremity of the middle temporal sulcus.

The Occipital Lobe. The occipital lobe is situated at the occipital pole of each hemisphere. It is generally pyramidal in shape and presents a richly convoluted lateral surface. In apes this is separated from the parietal lobe by the sulcus simiarum. The occipital surface is further subdivided by a transverse furrow, the transverse occipital sulcus, which appears most distinctly in the fetus. Subsequently it joins the occipital portion of the intraparietal sulcus of which it appears to be the bifurcated caudal extremity. In apes it is concealed by the caudal operculum, but on separating the convolutions bordering upon the sulcus simiarum, it is seen on the anterior wall of the sulcus. A lateral occipital sulcus extends obliquely backward for a short distance below the lateral end of the transverse occipital sulcus toward the occipital pole of the hemisphere. The calcarine fissure, one of the chief landmarks on the mesial surface, often extends backward upon the mesial surface of the occipital lobe to its pole where it bifurcates to form the fissura extrema of Seitz, visible when the hemisphere is viewed from its occipital aspect.

The Temporal Lobe. The temporal lobe presents a lateral surface which is bounded for two-thirds of its length by the horizontal portion of the Sylvian fissure. At the caudal extremity of this fissure the lobe is continuous with the parietal and occipital lobes. Two variable fissures appear on the lateral surface of the temporal lobe, the superior and middle temporal sulci. An inferior temporal sulcus is seen upon the ventral surface of the lobe extending caudally toward the occipital pole. The convolutions upon the surface of the temporal lobe are three in number, the superior temporal, the middle temporal and the inferior temporal gyres, all of which may be easily discerned in this portion of the brain in the great anthropoids, to a less extent also in some of the still lower primates. The disposition of the convolutions in relation with the upturned end of the superior and middle temporal sulci has already been described and is important in that it gives these areas of the cortex a greater convolutional richness than is true of any of the great anthropoids.

SIGNIFICANCE OF CONVOLUTIONAL COMPLEXITY IN THE HUMAN BRAIN

If a single statement might cover the characteristic features of the lateral aspect of the human hemisphere in contrast to all other primates, it is that the complexity of the convolutions and the tortuousness of the fissures render impossible a uniform description in man, while the relative simplicity of these features in all simian brains discloses the discrete territorial boundaries almost at first glance.

Although the human brain has made great advance in its relative weight when compared with the anthropoid brain, both absolutely and in relation to body weight, its chief superiority lies in its intricate complexity of convolutional arrangement. As applied to the frontal area this observation becomes particularly forceful. The frontal lobe, often spoken of as the silent area, is, as a matter of fact, now credited with such functions as those connected with the regulation of the higher faculties of the mind, the development of personality, the formation of all those associational memories which enter into and form personal experience and thus bespeak the degree of intellectual development. A similar convolutional expansion of the occipital lobe is an indication of the extent to which visual function has extended its associational significance and the added degree in which it contributes to the general synthesis of sensory combinations entering into the experience of the individual. That the temporal and parietal lobes have been somewhat outrun by the expanding complexity of the frontal and occipital lobes is perhaps not surprising, inasmuch as these two intermediate areas of the brain have always presented a certain predominance because of the representation within their cortical areas of somesthetic sensibility and the sense of hearing. It must not be inferred from this observation that there are not definite advances in these types of sensory organization of man, but merely that the progress made in this department of neural specialization is less conspicuous than that in the frontal or occipital lobe. Somesthetic sensibility, as well as the sense of hearing, have always played prominent rôles in the organization of the general sensorium. Undoubtedly the degree of efficient elaboration in both the temporal and parietal regions, as far as they concern the sense of hearing and general body sense, is in man much more advanced in its capacity than in any of the other primates. From the purely structural standpoint this advance seems less pronounced because it is so greatly overshadowed by the remarkable expansions which have gone forward in the frontal lobe and to a slightly less degree in the occipital lobe.

THE BASAL SURFACE OF THE BRAIN

The basal surface of the brain presents features less striking than those seen upon the lateral convexity. This surface in its more anterior portion is in relation with the anterior fossa of the skull and rests upon the orbital plate of the frontal bone. It is for this reason called the orbital surface.

The Orbital Surface of the Frontal Region. The general expansion of the frontal region of the brain is again indicated by the modifications of this area. The orbital concavity, so conspicuous in the lower and intermediate primates and gradually becoming less prominent in the great anthropoids, in man has decreased considerably. While it is still recognizable, in some human brains it is often difficult to discern any such concave disposition in the orbital surface. It is true that the brain makes an impression upon the orbital plate rather than that this plate indents the orbital surface. It is possible to recognize in the bony structure forming the floor of the anterior fossa, actual digitations caused by impressions of the orbital convolutions, known for this reason as *digitationes orbitales*. This entire modification is consonant with other evidences of expansion in the frontal lobe of the human brain. It is a feature of the utmost importance in distinguishing the encephalon of man from all other species. Inasmuch as the frontal lobe is looked upon as the area in which the highest syntheses of neural impulses are composed (the gallery of human experience), it is evident that its extreme expansion in man is in direct proportion to his needs in these important features of his organization. The olfactory tract and bulb are readily detachable as far back as the trigonum olfactorium, and such detachment reveals the deep, olfactory sulcus, which in many instances extends forward around the frontal pole of the brain to become continuous with a small extension of the superior frontal fissure. The increase in size and prominence of this fissure is another instance of extension in the frontal lobe. In some cases this olfactory sulcus extends only as far forward as the frontal pole in one hemisphere, but in the opposite hemisphere may attain its continuity with the superior frontal sulcus. By means of the olfactory sulcus, a well-defined gyrus rectus is delimited from the adjacent orbital convolutions. In those instances in which the olfactory sulcus is continuous with the superior frontal fissure, the gyrus rectus then becomes the orbital expression of the superior frontal convolution. All of the brain features observed in the great anthropoids and even in lower and intermediate primates, which in these inferior forms present themselves as incipient landmarks, have in the human brain attained their full representation. Thus the process of evolution which had its inception in the more primitive anthropoid organization finds its ultimate expression in man.

The Chiasm. The chiasm shows an angulation with reference both to the nerves and the tracts which identifies it with this region of the anthropoid brain. Upon the base, however, in the region immediately caudal to the chiasm, the optico-peduncular space in man appears to be much more conspicuous, by the fact that this region is larger and that its contents are more easily discerned. It includes the tuber cinereum, the area of attachment of the stalk of the infundibular process and the mammillary bodies. The increased prominence of the cerebral peduncles is significant of expansion

FIG. 339A. LEFT LATERAL SURFACE OF BRAIN, HOMO SAPIENS.
Actual Length 173 mm

in those great projection systems connected with the cerebral hemispheres. The pallio-ponto-cerebellar tracts, as well as the pyramidal tract, are the constituents of the peduncle. Expansion in these tracts accounts for the increased size of the peduncle.

Occipital Surface of Basilar Portion of Hemisphere. The occipital surface of the basilar portion of the hemisphere shows certain equally striking modifications in contour. This is especially notable in that the cerebellar concavity, like its cephalic counterpart in the orbital region, has undergone reduction in size and prominence. Only a slight remnant of this depression appears in the region immediately posterior to the corpus callosum. The [illegible] which is much reduced in size, and the degree to which the [illegible] the cerebellum has undergone considerable [illegible]

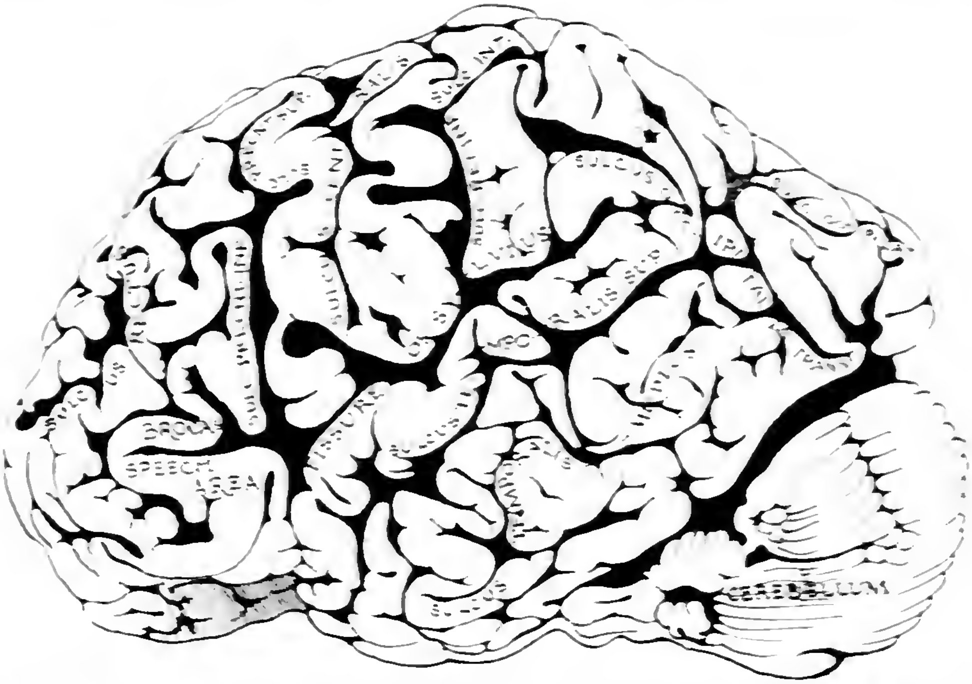


FIG. 292 B. DETAILED DIAGRAM OF LEFT LATERAL [illegible] OF BRAIN [illegible] HOMO SAPIENS.

[illegible]

higher anthropoids. All of these facts indicate a [illegible] both in the occipital region of the hemispheres and in the [illegible]. The latter, however, is most marked [illegible]

THE CEREBELLUM

The cerebellum [illegible] evidence of [illegible] in the human brain [illegible] tentorial surface of the cerebellum which has lost much of its transverse convexity. It manifests none of that sharp gabling so prominent in the lower and intermediate primates. Even the ridge-pole effect produced by the vermal portion of the cerebellum is almost completely lost, and while this cerebellar surface is not actually flat, it much more nearly approaches this condition than in any of the forms already described. The most cephalic portion of the superior vermis is still somewhat protrusive, extending slightly above the general plane of the tentorial surface. The interfolial sulci pass almost without demarcation from vermis to lateral lobes and the folial delineation is, if anything, slightly more pronounced than in the lower species. This cerebellar expansion, which appears to have confined itself so largely to the lateral lobes, accords with the expansion discernible in the cerebral hemispheres. It offers a convincing argument as to the pronounced increment in the several functional areas of the encephalon. The indications of expansion evident upon the tentorial surface of the cerebellum become more pronounced on the occipital surface. The posterior cerebellar notch has become deep and the vallecula so much depressed below the surface that it requires a separation of the lateral masses of the cerebellum to reveal the now almost concealed inferior vermis. The two apposite borders of the lateral cerebellar lobes are in contact with the falx cerebelli. The appearance of this surface gives such outstanding prominence to the lateral lobes as to make the vermal portion of the organ seem almost insignificant. When the lateral lobes are separated, two deep paramedian sulci are brought to view, which apparently interrupt the continuity of the vermal sulci as they pass into the lateral lobes. Upon the petroso-ventricular surface of the cerebellum, all of the usual landmarks are prominent, including the cerebello-pontile angle, the great horizontal fissure and the middle peduncle. In every feature, this portion of the brain, which has its prototype in the brains of all lower primates, reaches its greatest definition in man.

IMPRESSION GAINED FROM A SURVEY OF THE EXTERNAL SURFACE OF THE BRAIN

The impression gained from a survey of the external surface of the brain is that of a pronounced expansion in all those parts particularly concerned with the functions over which the neopallium presides. These additions are all in the interest of neokinesis. Expansions in the parietal lobe for the increase of somesthetic sensibility enrich kinesthetic association in the control of motion. Expansions of the occipital lobe extend the realm of the visual sphere, not alone for sensory interpretation but equally for those contributions which vision makes to the regulation of the more highly organized skilled movements. Enlargement of the temporal lobe extends the sphere of auditory perception to bring into existence those combinations of neural impulses advantageous alike to the acquisition and the maintenance of skilled performances; and finally, the most notable expansion of all is in the frontal lobes for the upbuilding of a neural mechanism essential to the organization of personality, the construction of judgment and of all the higher faculties of discrimination and those far-reaching [illegible] in adjustment to this complex environment. A similar expansion [illegible] of augmented function appears [illegible].

SURFACE LANDMARKS OF THE BRAIN STEM

As is the case with the cerebral hemispheres, [illegible] marks become better defined [illegible] stem. The [illegible] the medulla presents [illegible] more caudal portion is interrupted [illegible] decussation. This decussation [illegible] than in the lower forms. On either side [illegible] pyramids, their apices [illegible]. A[illegible] pre-olivary sulcus separates the pyramid from a prominent olivary eminence. A distinct postolivary sulcus intervenes between the olivary body and the spinocerebellar eminence, the expression of which latter is delimited dorsally

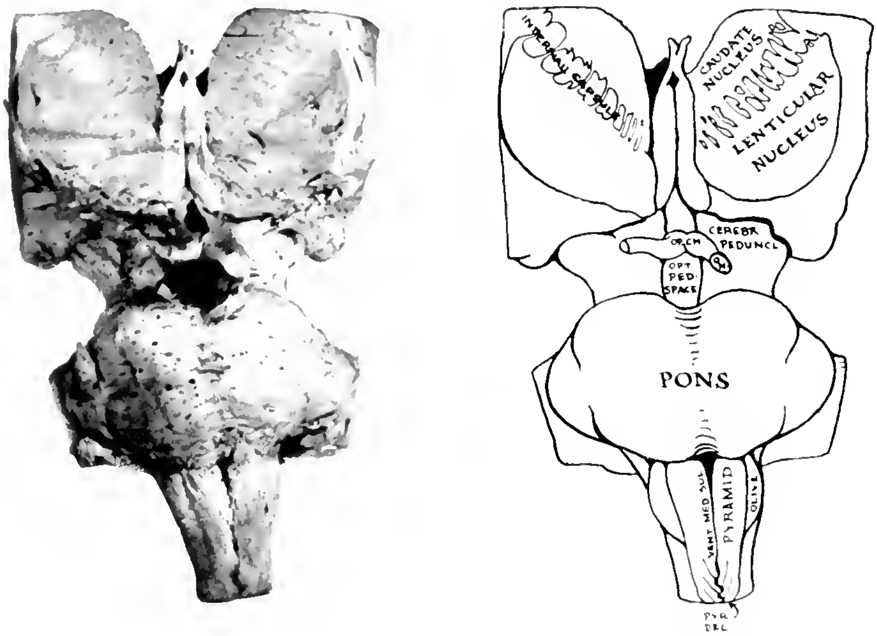


FIG. 340. VENTRAL SURFACE OF BRAIN STEM, HOMO SAPIENS.
[Actual Length 82 mm.]

KEY TO DIAGRAM. OP. CH., Optic Chiasm; O. N., Optic Nerve; OPT. PED. SPACE, Opticopeduncular Space; PYR. DEC., Pyramidal Decussation; VENT. MED. SUL., Ventromedial Sulcus.

by a well-defined intermediate sulcus. The most striking feature on the ventral surface of the brain stem in man is the marked prominence of the pons. This structure has gained in all dimensions. It is separated from the oblongata by the bulbopontile sulcus.

The cerebral peduncles, like the pons Varolii, are strikingly prominent in man. They are longer and more marked in their surface relief. All of the features upon the ventral surface of the brain stem, including more particularly the prominence of the pyramid, the pons Varolii and the cerebral peduncles, suggest the great advances which the human brain has made in the organization of neokinetic control. The large pyramid serves for the conveyance of motor impulses from the cortex which controls somatic

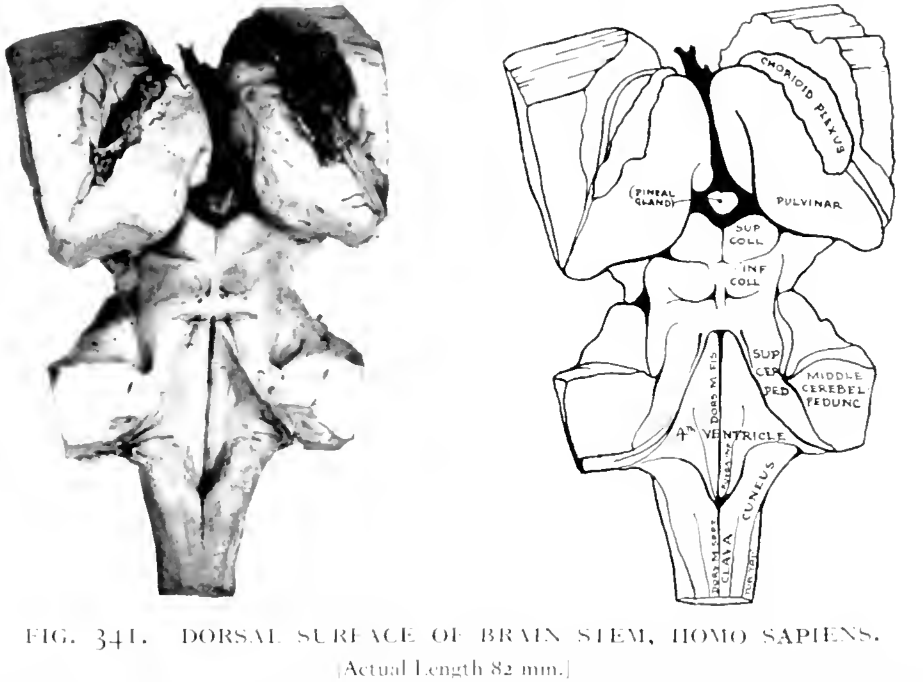


FIG. 341. DORSAL SURFACE OF BRAIN STEM, HOMO SAPIENS.

[Actual Length 82 mm.]

KEY TO DIAGRAM. DORS. M. FIS., Dorsomedian Fissure; DORS. M. SEPT., Dorsomedian Septum; FOVEA INF., Fovea Inferior; INF. COLL., Inferior Colliculus; MIDDLE CEREBEL. PEDUNC., Middle Cerebellar Peduncle; SUP. CER. PED., Superior Cerebellar Peduncle; SUP. COLL., Superior Colliculus; TUB. TRIG., Tuberculum Trigemini.

activity. The pons has a somewhat similar significance since it represents those fibers which connect the cerebral hemispheres with the lateral lobes of the cerebellum. The cerebral peduncles express both the connection between the cerebral hemispheres and the spinal cord in the interest of voluntary control, and the pallio-ponto-cerebellar association in relation to coordination.

The dorsal surface of the oblongata gives further emphasis to the advances in the human brain. The claval eminence (column and nucleus of Goll) is separated by the dorsal paramedian sulcus from the cuneus (column and nucleus of Burdach). A dorsolateral sulcus separates the cuneus from a well-defined eminentia trigemini. These three elevations of the dorsal surface constitute the major elements entering into the dorsal sensory field. In relative size the column of Burdach has increased in its diameters as compared with the column of Goll. This expansion indicates an increment in the influx of sensory impressions from the upper extremity and hand as compared with those making their way brainward from the lower extremity and foot. At their cephalic extremity the clava and cuneus become reduced in their surface relief. The cuneus extends further cephalad than the clava and at the level of the lateral recess of the ventricle reaches the general plane of the ventricular floor. The superior angle of the fourth ventricle is bounded upon either side by the middle and superior cerebellar peduncles and decreases in size as it approaches the caudal orifice of the Sylvian aqueduct. The floor of the fourth ventricle thus outlined consists of two triangles, the inferior triangle bounded by the cuneus and clava, and the superior triangle bounded by the middle and superior cerebellar peduncles.

At the caudal angle of the fourth ventricle the divarication of the alar plates is indicated by a remnant of the gray matter, the obex. The floor is divided into two symmetrical halves by a median sulcus which runs from the apex of the lower triangle to the apex of the upper triangle. A second sulcus starts beneath the obex lateral to the median sulcus, and proceeds cephalad. It is situated about midway between the median sulcus and the lateral wall. This is the *sulcus limitans* which divides the floor of the ventricles into a mesial motor portion derived from the basal plate, and a lateral sensory portion derived from the alar plate. At the caudal angle of the ventricle immediately adjacent to the midline is a long narrow elevation, the eminentia hypoglossi, which indicates the cephalic extremity of the hypoglossal nucleus. Cephalad to the eminentia hypoglossi and upon either side of the median sulcus is a less prominent elevation, the eminentia fasciculi teretis. In a posi-

brain is a well-defined mesial geniculate body connected with the inferior colliculus by means of the brachium conjunctivum posticum. The decrease in prominence of the collicular eminences in the roof of the midbrain is significant of that general transference of visual and auditory function which has been in process throughout the primate series. It attains its ultimate expression in man. Confirmatory evidence of this supersedence of the midbrain tectum by the areas in the cerebral hemispheres is easily obtained by a survey of those regions in the cerebral cortex assigned to the functions of hearing and vision.

Internal Structure of the Brain Stem

It is difficult to approach the description of the internal structure of the human brain without a certain feeling of conviction that the sections clearly depict the culmination of that evolutionary process which has been traced from its primate beginnings. What is most impressive about these sections of the human brain is the fact that every feature hitherto seen in the apes comes at length to its sharp and final focus. The entire brain stem, like the hemispheres, manifests an enlargement which seems somewhat out of proportion to the stature of man. The oblongata, the pons Varolii and the midbrain have a little less than twice the dimensions of the corresponding structures in gorilla, an animal which in point of size is considerably larger than man.

LEVEL OF THE PYRAMIDAL DECUSSATION (FIG. 342)

Here the features are those familiar throughout the entire primate series incident to the decussation of the pyramidal fibers. The section shows the ventromedian sulcus, somewhat deflected to one side under the influence of the crossing fibers. On its dorsal aspect is a long dorsomedian septum extending from the surface into the central gray (Cen). The pyramid, occupying its usual ventromesial position (Py), is undergoing decussation, and its crossing fibers, passing from right to left, have separated the ventral gray column (Ven) from the central gray matter (Cen). Some

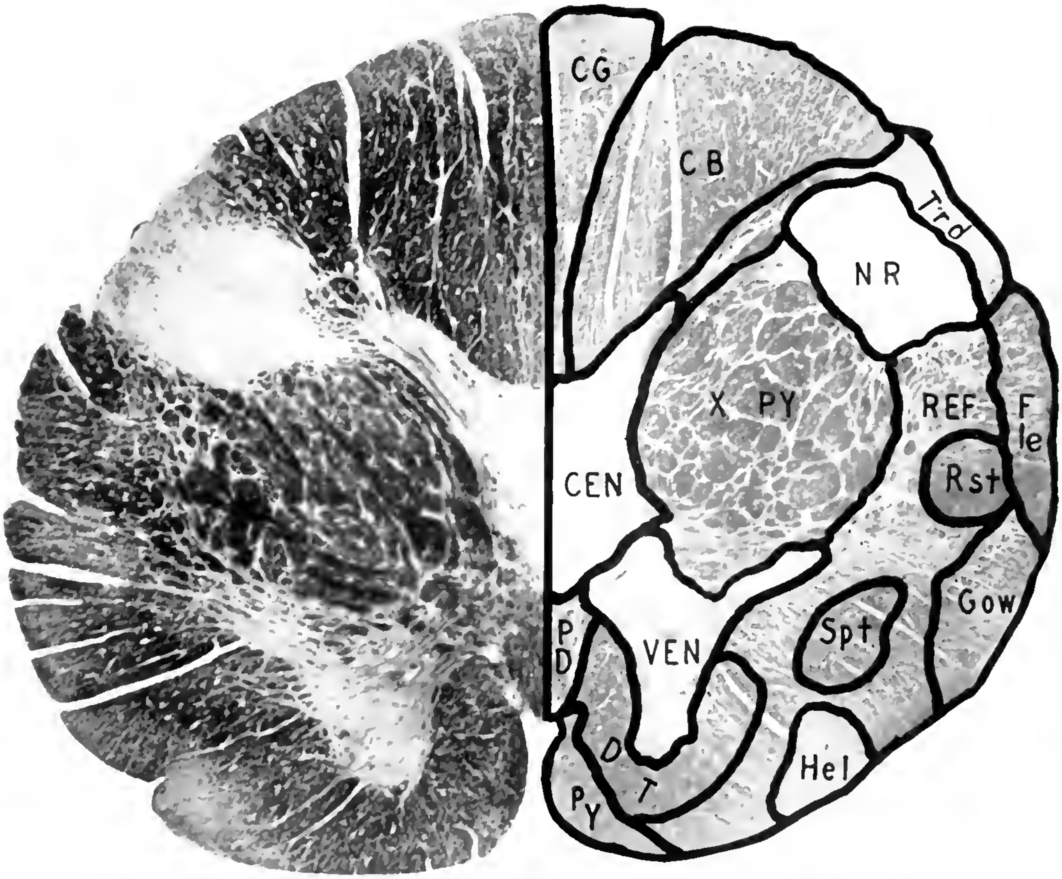


FIG. 342. MAN. LEVEL OF THE PYRAMIDAL DECUSSATION.

CB, Column of Burdach; CEN, Central Gray Matter; CG, Column of Goll; DT, Deiterso-spinal Tract; FLE, Dorsal Spinocerebellar Tract; GOW, Ventral Spinocerebellar Tract; HEL, Spino-olivary Tract of Helweg; NR, Nucleus of Rolando; PD, Predorsal Bundle; PY, Pyramid; REF, Reticular Formation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; TRD, Descending Trigeminal Tract; VEN, Ventral Gray Column; XPY, Crossed Pyramidal Tract. [Accession Man Section N 55. Actual Size 10 × 7 mm.]

idea concerning the extensiveness of the pyramidal system may be obtained from the massiveness of the decussation as the fibers interpose themselves between the central gray and the ventral gray column. The latter seems to retain many of the characteristics of the ventral horn in the spinal cord, and were it not for its detachment by the crossing pyramidal fibers, the general appearance of the section in this respect would correspond closely to that of the upper cervical region of the cord. The central gray matter is somewhat broader and more massive than in the lower levels of the axis. It contains near its center the central canal. It has not manifested as yet any of its tendency toward dorsal migration in preparation for the opening of the fourth ventricle. Dorsolaterally it is connected by a slender cervix with a dorsal gray column, surrounding the periphery of which is the substantia gelatinosa (NR). This substance has much increased in size and has moved into a more lateral position as compared with its conditions in the spinal cord. It is beginning to occupy the position which gives rise at higher levels to the eminentia trigemini.

The dorsal sensory field exhibits the wide expanse lying between the two laterally deflected masses of the substantia gelatinosa. The most striking feature in it, however, is the proportion of the mesial column of Goll (CG) to the more lateral column of Burdach (CB). These two fasciculi of densely myelinized fibers are separated from each other by a well-defined dorsal paramedian sulcus. There is thus no difficulty in distinguishing the boundaries of the area representing the sensory influx from the leg and foot and of that serving in a similar capacity for the arm and hand. The columnar representative of the lower extremity, the column of Goll, is about one-third the size of the similar representative of the upper extremity and hand, the column of Burdach. None of the primates shows with such decisiveness the delimitation between these two columns, nor is there any case in which the disparity in size between them is more marked than in man. This difference denotes a marked increase in the functional importance of those sensory afferents connected with the upper extremity and hand. It is by no means implied that the morphological differentiation in the hand

and upper extremity has so progressed over and above the adaptive changes manifest in the leg and foot that this differentiation de facto explains the disparity in size between the two sensory columns. If the structural differentiation alone were the determining motive in the expansion which occurs in the column of Burdach, it is probable that no such disparity would be evident. The greater size of the fasciculus cuneatus must be attributed more to the functional expansion arising in connection with the wide increase in range of movement now possible in the hand. The total number of postures and muscular combinations of myotensional states for fineness of movement in the human upper extremity has shown a pronounced increase as compared with any of the other primates. This large number of joint and muscle combinations incident to complex manual manipulation in man has called forth a corresponding increase in the sensory influx. Although in the great anthropoids there has been a marked tendency to establish a similar difference in the size of the columns of Goll and Burdach, thus signifying that the forelimb was becoming progressively more emphatic in its influence as a sensory organ, the final stage is reached in man. The contrast is most convincing on comparing the human conditions with such low forms as the tarsius or marmoset. The nervous system reflects in these particulars the modifications occurring in the upper extremity and hand.

Another feature deserving emphasis is the fact that the entire sensory field is considerably larger than in the lower primates. The total sensory influx from the extremities, both upper and lower, appears to be of larger volume in man than in apes.

Lateral to the column of Burdach is the substantia gelatinosa trigemini (NR) on whose outer margin is the descending trigeminal tract (Trd). The reticular formation (Ref) is well defined and lies in a position dorsal to the ventral gray column. In the circumferential and intermediate zones in the medullary substance are the two ascending spinocerebellar tracts (Flc, Gow), the spinothalamic (Spt), rubrospinal (Rst) and Deiterso-spinal (DT), tracts together with the usual juxtagriseal intersegmental association fibers. In the ventrolateral region is the spino-olivary tract of Helweg (Hel).

LEVEL OF THE CAUDAL EXTREMITY OF THE DORSAL SENSORY NUCLEI (FIG. 343)

At this level the changes are those incident to the appearance in the dorsal sensory field of the nuclei of Goll (NG) and of Burdach (NB). The pyramidal decussation is still in process at this level as indicated by the marked deflection of the ventromedian sulcus. The reticular formation (Ref) has increased in size as compared with the lower level, so much so that the cephalic remnant of the ventral gray column (Ven) is now connected by many griseal bridges with the central gray matter (Cen). The latter structure has migrated somewhat dorsally in the general movement which takes place in preparation for the opening of the fourth ventricle. The dorsal sensory columns of Goll and Burdach still show their exact demarcation by means of the dorsal paramedian sulcus. The column of Goll is about one-third the size of the column of Burdach. In both of these columns there now appears the corresponding nuclear structure. The nucleus of Burdach is a protrusion of the central gray matter into the investing medullary substance of Burdach's column. The nucleus of Goll occupies a more independent position almost entirely surrounded by medullary substance. The substantia gelatinosa of Rolando (NR) shows some increase in dimensions as compared with the last level, and the descending trigeminal tract (Trd) is also obviously larger. The central gray matter (Cen) is roughly triangular in shape with its base directed toward the dorsal aspect of the stem. Its triangular form is in part accounted for by the decussating fibers of the pyramidal system (Pyx). The cervix of the dorsal gray column is represented only by a few gray bridges connecting the substantia gelatinosa trigemini with the central gray matter. The pyramid occupies its customary ventromesial position although its outline is not clearly defined due to diffusion incident to the crossing of pyramidal fibers. The circumferential and intermediate zones

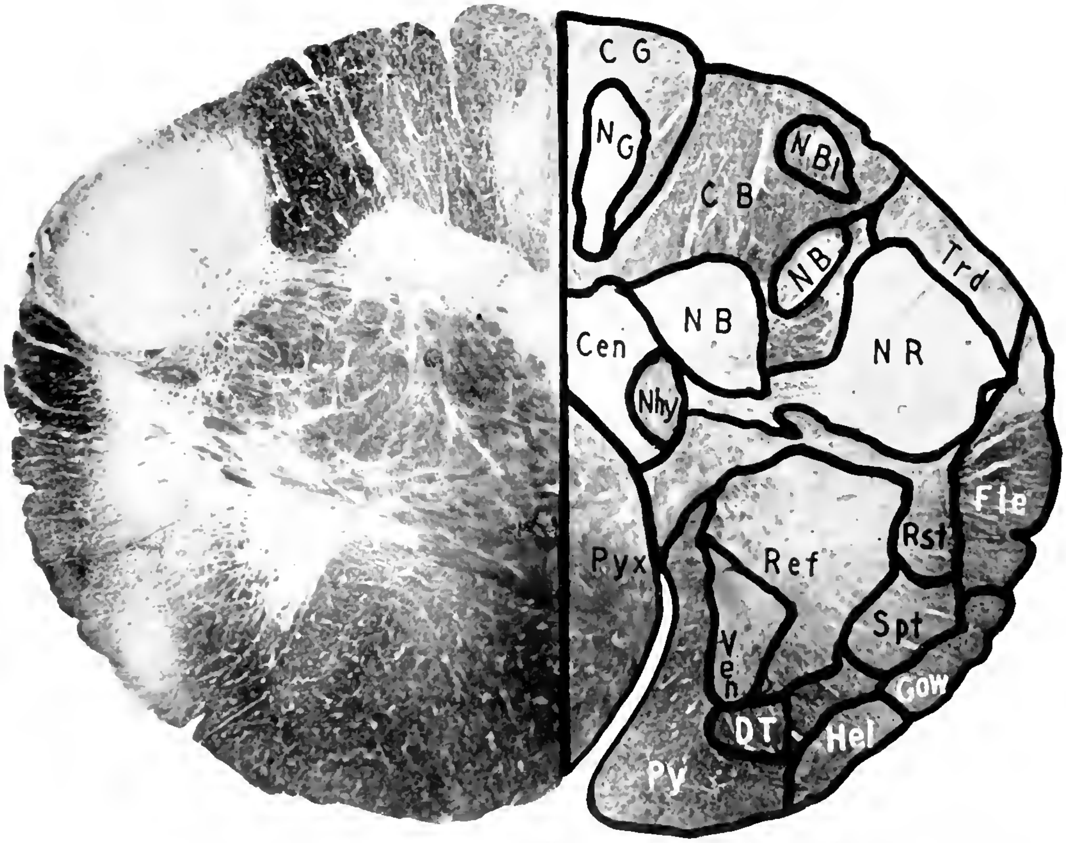


FIG. 343. MAN. LEVEL OF CAUDAL EXTREMITY OF DORSAL SENSORY NUCLEI.

CB, Column of Burdach; CEN, Central Gray Matter; CG, Column of Goll; DT, Deiterso-spinal Tract; FLE, Dorsal Spinocerebellar Tract; GOW, Ventral Spinocerebellar Tract; HEL, Spino-olivary Tract of Helweg; NB, Nucleus of Burdach; NBL, Nucleus of Blumenau; NHY, Hypoglossal Nucleus; NG, Nucleus of Goll; NR, Nucleus of Rolando; PY, Pyramid; PYX, Pyramidal Decussation; RET, Reticular Formation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; TRD, Descending Trigeminal Tract; VEN, Ventral Gray Column. Accession Man. Section N 175. Actual Size, 13 × 10 mm.]

show the same general arrangement as heretofore and contain on the periphery the two spinocerebellar tracts (Fle, Gow) and in the intermediate area, the rubrospinal (Rst), spinothalamic (Spt) and Deitersospinal (DT) tracts.

LEVEL OF THE CAUDAL EXTREMITY OF THE INFERIOR OLIVARY NUCLEUS (FIG. 344)

Here the general configuration of the section has changed considerably due to expansion incident to the dorsal migration of the central gray matter. In the ventral position, occupying the usual place on either side of the ventromedial sulcus, are the dense bundles of the pyramids (Py). It is possible at this level to obtain some estimation of the relative importance of the pyramidal system in the human neuraxis. At this level the pyramidal fibers occupy at least a quarter of the entire cross section. This clearly indicates to what extent the function of volitional control over somatic musculature has expanded to meet new demands imposed by the human race. The pyramidal system has progressively increased from the lowest extremity of the primate series to this point.

Dorsolateral to the pyramid is a mass of gray matter heretofore not apparent in the section, the caudal extremity of the inferior olivary nucleus (IO). The central gray matter (Cen) has become more circular in outline, containing the central canal near its center. It is almost entirely surrounded by arching medullated fibers rising for the most part from the nucleus of Goll and sweeping to the raphe to form the lower portion of the decussation of the mesial fillet (Mfx). These arching axons are the internal arcuate fibers and represent the decussation in the pathway for the conduction of impulses from the leg and foot. The dorsal sensory field shows in this section as in lower levels the disproportion between the column of Goll and column of Burdach. These two dorsal columns are still clearly demarcated by the dorsal paramedian sulcus. In the most lateral position of the dorsal sensory field is the substantia gelatinosa trigemini or nucleus

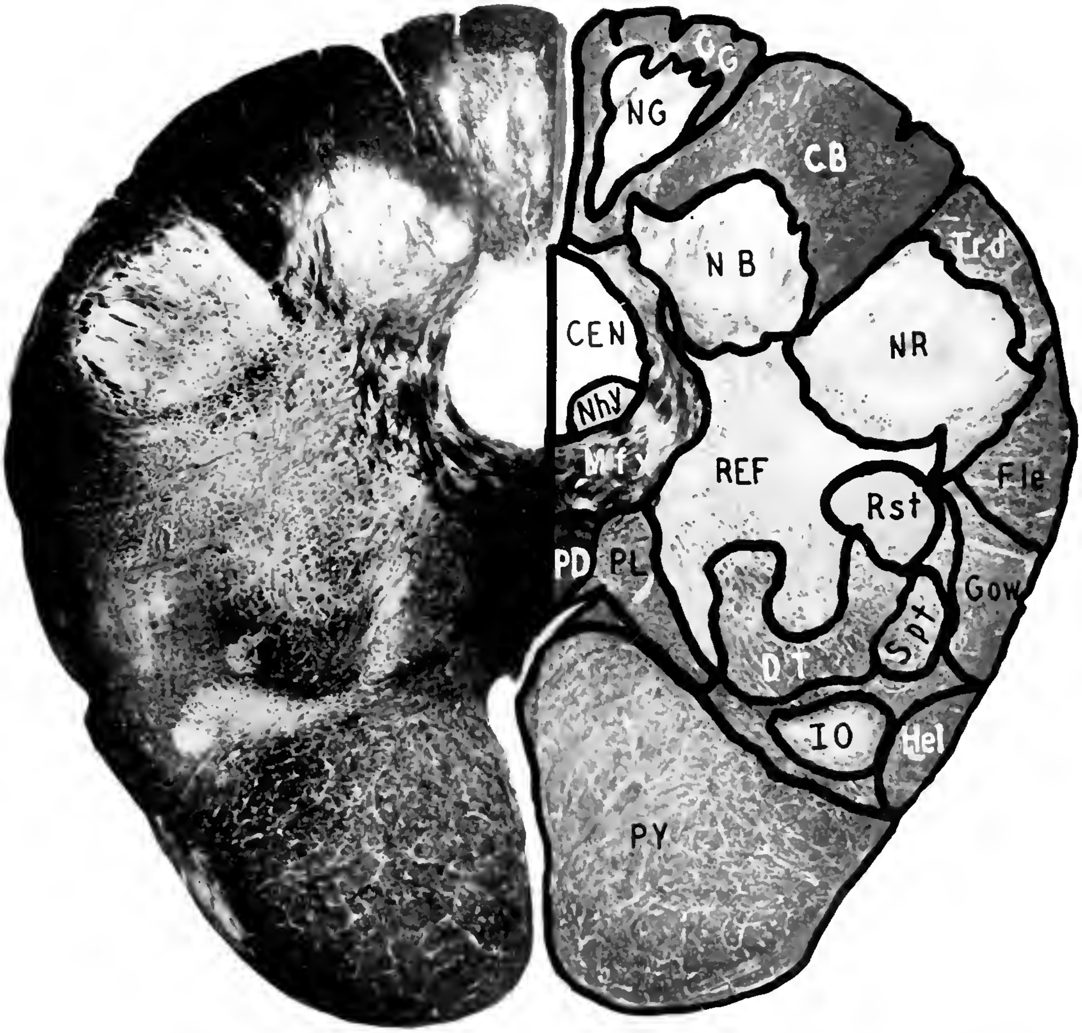


FIG. 344. MAN. LEVEL OF CAUDAL EXTREMITY OF INFERIOR OLIVARY NUCLEUS.

CB, Column of Burdach; CEN, Central Gray Matter; CG, Column of Goll; DT, Deiterso-spinal Tract; FLE, Dorsal Spinocerebellar Tract; GOW, Ventral Spinocerebellar Tract; HEL, Spino-olivary Tract of Helweg; IO, Inferior Olive; MFX, Crossing of the Mesial Fillet; NB, Nucleus of Burdach; NG, Nucleus of Goll; NHY, Hypoglossal Nucleus; NR, Nucleus of Rolando; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PY, Pyramid; REF, Reticular Formation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; TRD, Descending Trigeminal Tract. Accession Man. Section N 250. Actual size 13 × 8 mm.

of Rolando (NR), upon whose outer margin is the descending trigeminal tract (Trd). A few scattered collections of gray matter in the column of Burdach represent the caudal extremity of the accessory nucleus of Blumenau, also called the lateral nucleus of Monakow.

The circumferential and intermediate zones contain as heretofore the two ascending spinocerebellar tracts (Fle, Gow) on the periphery, and mesial to them the rubrospinal, spinothalamic and Deiterso-spinal tracts (DT, Rst, Spt).

LEVEL THROUGH THE MIDDLE OF THE INFERIOR OLIVARY BODY (FIG. 345)

At this level the changes in the external configuration are those incident to the opening of the fourth ventricle and the appearance of the inferior olive in its full development. The dorsal aspect of the section has increased in its diameter corresponding to the opening of the ventricular space. In a similar manner the ventral diameter has increased due to the appearance of the inferior olivary body. Occupying their usual position in the ventromesial portion of the section are the two pyramids separated by a wide ventromedian sulcus. Along the ventral margin of the pyramid a nuclear mass has made its appearance, the nucleus arciformis. Dorsal to the pyramids is the collected mass of axons forming the mesial fillet (Mf), to which a number of internal arcuate fibers are still making their way from the cephalic extremity of the nucleus cuneatus. The inferior olivary nucleus has its characteristic human appearance. It is distinctly outlined and much convoluted in form, with its two accessory olivary elements, the dorsal accessory olive (DO) and the mesial accessory olive (VO), adjacent to it. This increase in the volume, in the definition and in the degree of convolution of the inferior olive carries this structure to its highest degree of differentiation seen in mammals. Slowly and by progressive stages this structure has advanced through all intermediate phases from the lowest of the primates until it reaches its culmination at this point. It seems fair to say that no structure in the human body shows more clearly the expansive unfolding and progressive specialization indicative of an evolutionary process

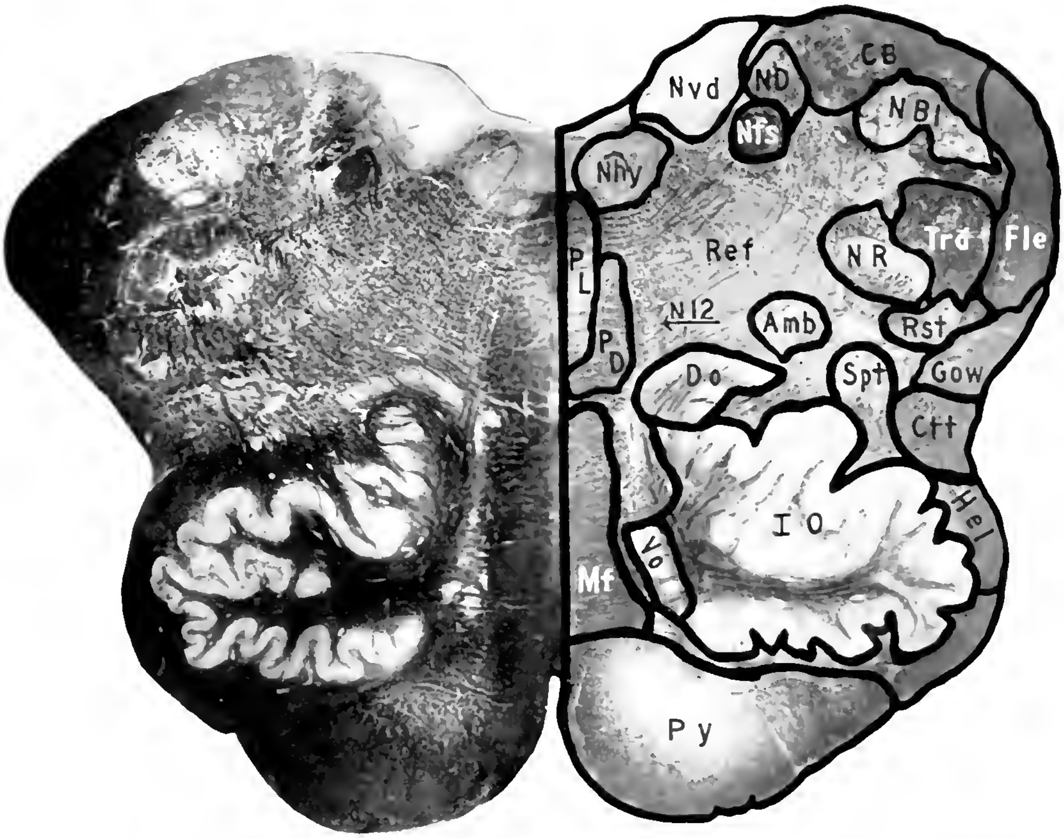


FIG. 345. MAN. LEVEL THROUGH MIDDLE OF INFERIOR OLIVARY BODY.

AMB, Nucleus Ambiguus; CB, Column of Burdach; CTT, Central Tegmental Tract; DO, Dorsal Accessory Olive; FLE, Dorsal Spinocerebellar Tract; GOW, Ventral Spinocerebellar Tract; HEL, Spino-olivary Tract of Helweg; IO, Inferior Olive; MF, Mesial Fillet; NBL, Nucleus of Blumenau; ND, Nucleus of Deiters; NFS, Solitary Nucleus; NHY, Hypoglossal Nucleus; NR, Nucleus of Rolando; NVD, Dorsal Vagal Nucleus; N12, Twelfth Cranial Nerve; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PY, Pyramid; REF, Reticular Formation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; VO, Ventral Accessory Olive. [Accession Man. Section N 433. Actual Size 20 × 11 mm.]

than the inferior olivary nucleus. Starting as an ill-defined aggregation of gray matter in the ventrolateral quadrant of the oblongata of lemur, this great nucleus of the brain stem has manifested the progressive modifications seen in the intermediate primates. At length in the great anthropoids it begins to disclose that outline familiar both in configuration and definition which finally is expressed in the richly convoluted nucleus of the human brain. Assuming the correctness of the interpretation already ascribed to the inferior olivary nucleus in its relation to the simultaneous movements of the head, eye and hand as well as the facilitating of all skilled movements, it will be clear that a functional expression of this expansion in the primate order has kept pace with the structural evolution of the nucleus. For example, the skilled performances of man in which simultaneous movements of the eyeball, the hand and the head are essential, as compared with those of the lemur or marmoset, appear to be greatly in advance of such acts in these lower primates.

The body of the central gray matter has completed its dorsal migration and lies in a position forming the floor of the fourth ventricle. In its ventromesial portion is the clearly differentiated hypoglossal nucleus (N hy), separated from which by the funiculus separans is the dorsal vagal nucleus (N vd). The emergent fibers from the twelfth nerve (N 12) make their way forward from the nucleus toward the inferior olivary body, while the entering fibers of the vagus nerve pass through the lateral aspect of the periphery and make their way to the dorsal sensory nucleus. They traverse in so doing the restiform body, the descending trigeminal fasciculus and the substantia gelatinosa of Rolando (N R). Ventrolateral to the dorsal vagal nucleus is a collection of densely myelinized fibers surrounded by a nuclear mass. This comprises the nucleus solitarius (N fs) and its accompanying fasciculus solitarius. In the most lateral position in the dorsal field is the cephalic extremity of the nucleus of Blumenau (N Bl) surrounded by a few myelinated fibers arising in the column of Burdach. Peripheral to this is the dense myelinized bundle constituting the restiform body (F le) and ventral to the nucleus of Burdach is the substantia gelatinosa trigemini (N R) invested on its outer surface by the descending trigeminal tract (Trd).

This level represents a critical region in the brain stem. The nucleus of Burdach is replaced by another nuclear structure which also receives proprioceptive fibers but in this case coming from the highly specialized proprioceptors of the vestibular portion of the internal ear. The section is also critical as showing the approach to the next higher segment of the axis represented by the pons Varolii. The transition which is about to occur is indicated on the ventral surface by the appearance of the nucleus arciformis. In man this nucleus which appears to be the caudal expression of the exuberant pontile nuclei extends much further downward along the axis than is the case in the other anthropoids. (See reconstruction of human stem.)

LEVEL OF THE VESTIBULAR NUCLEI (FIGS. 346, 347)

At this level the contour of the section shows those changes incident to the appearance in the dorsal sensory field of the large vestibular complex which now occupies the position formerly held by the nuclei of Goll and Burdach. The relief of this vestibular complex has previously been noted upon the floor of the fourth ventricle. Its general proportions and appearance in man give the impression of a structure somewhat less extensively developed than in the lower primates, and particularly in those forms which are highly specialized for arboreal life. It may be difficult to maintain that the vestibular nuclei in man are less extensive than in other primates. On the other hand, it would seem likely that the balancing mechanism in man had less demand made upon it than would be the case in those animals which lead arboreal lives. Man, with his more firm supporting base upon the ground, is provided with a surface which affords him greater security. There are reasons, however, why the balancing mechanism in man should not undergo marked reduction. These arise from the fact that, having assumed the erect posture, he walks upon two feet without aid or support from the upper extremities. Such is not the case in any of the apes which employ both the hands and the feet in their locomotion. Even those which

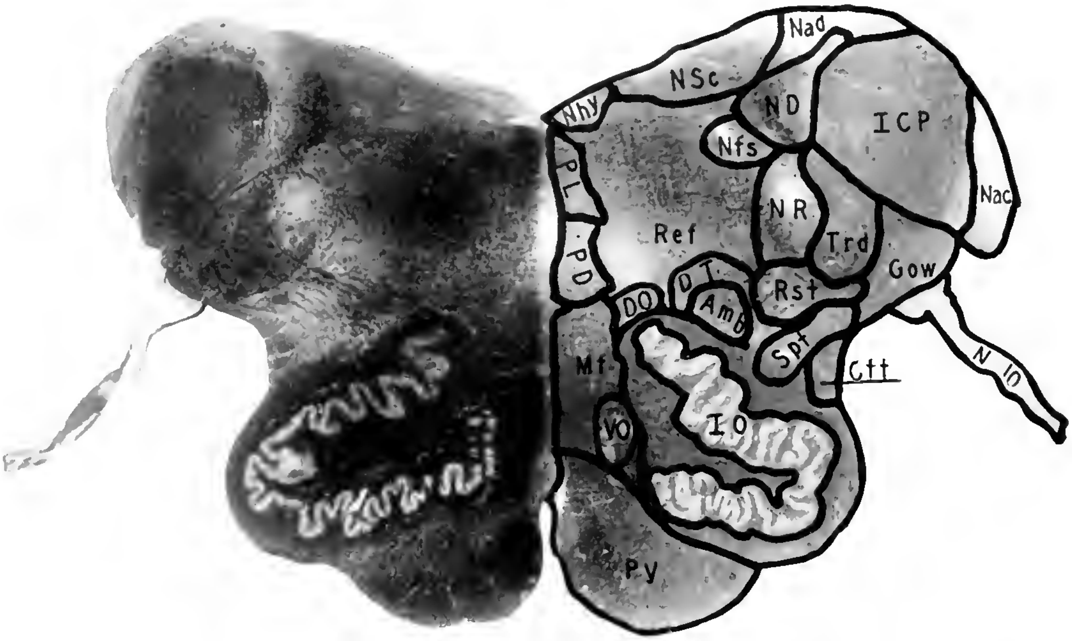


FIG. 346. MAN. LEVEL OF THE VESTIBULAR NUCLEI.

AMB, Nucleus Ambiguus; CTT, Central Tegmental Tract; DO, Dorsal Accessory Olive; DT, Deiterso-spinal Tract; GOW, Ventral Spinocerebellar Tract; ICP, Inferior Cerebellar Peduncle; IO, Inferior Olive; MF, Mesial Fillet; NAC, Ventral Cochlear Nucleus; NAD, Dorsal Cochlear Nucleus; ND, Deiters' Nucleus; NFS, Solitary Nucleus; NHY, Hypoglossal Nucleus; NR, Nucleus of Rolando; NSC, Schwalbe's Nucleus; N10, Vagal Nerve; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PY, Pyramid; RET, Reticular Formation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; TRD, Descending Trigeminal Tract; VO, Ventral Accessory Olive. [Accession Man. Section C 7. Actual Size 23 × 9 mm.]

have acquired something approaching the erect posture do, nevertheless, supplement their locomotor activities by using the hands either directly in contact with the ground or as balancing structures held outstretched over the head. An essential difference also in this connection is that the human hand has lost its foot-like characters while the feet have correspondingly become differentiated as locomotor organs devoid of prehensile specialization.

This far-reaching modification must have expressed itself in many profound alterations in the mechanism of locomotion and produced changes in the essential substratum of the balancing mechanism.

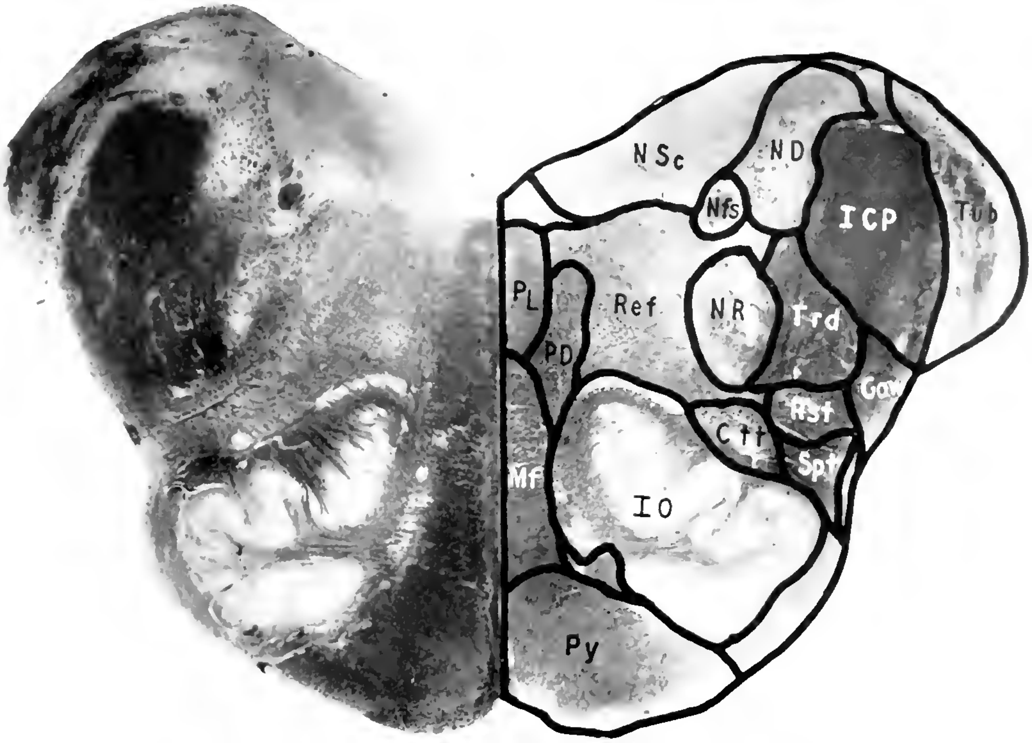


FIG. 347. MAN. LEVEL OF THE VESTIBULAR NUCLEI.

CTT, Central Tegmental Tract; GOW, Ventral Spinocerebellar Tract; ICP, Inferior Cerebellar Peduncle; IO, Inferior Olive; MF, Mesial Fillet; ND, Deiters' Nucleus; NFS, Solitary Nucleus; NR, Nucleus of Rolando; NSC, Schwalbe's Nucleus; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PY, Pyramid; RET, Reticular Formation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; TRD, Descending Trigeminal Tract; TUB, Tuberculum Acusticum. [Accession Man. Section C 180. Actual Size 22 × 12 mm.]

In man the vestibular complex consists of a small-celled triangular nucleus of Schwalbe (NSc) and a large-celled nucleus of Deiters (ND) scattered through which are many small bundles of heavily myelinized fibers. Entering fibers from the vestibular division of the eighth nerve make their way inward and pass through the ventral extremity of the restiform body to the nucleus of Deiters. Ventral to Deiters' nucleus is the somewhat reduced substantia gelatinosa trigemini (NR), and lateral to the nucleus is a massive bundle of fibers constituting the restiform body (ICP) about to establish final connections with the cerebellum. On the outer side of the restiform body is a mass of nuclear material penetrated by many nerve fibers. This is the tuberculum acusticum (Tub) which contains portions of the ventral and dorsal cochlear nuclei together with fibers arising in the cochlear division of the eighth nerve. The body of the central gray matter spreads across the floor of the ventricle. The specializations in the central gray substance are particularly concerned with the nuclei of the vestibular and cochlear divisions of the eighth nerve. The most mesial of these specializations is the triangular nucleus of Schwalbe (NSe).

At this level, the inferior olivary body appears in all its complex convolutional arrangement, showing a marked increase in volume as compared with the lower primates. It is associated with the dorsal and mesial accessory olives (DO, VO). Its fundus contains a mass of heavily myelinized axons from which many arcuate fibers pass across the midline of the raphe and make their way to the restiform body. These olivo-cerebellar connections are much more extensive than in anthropoids. They represent the only axons entering the inferior cerebellar peduncle and having diffuse distribution in the vermis and lateral lobes of the cerebellum. The circumferential zone, in contact with the inferior olive, contains the central tegmental tract (Ctt) which affords connection between the midbrain and the inferior olive. Whether this tract also has constituents which establish communication with still higher levels of the neuraxis, such, for example, as the interbrain, the corpus striatum and even the cerebral cortex, is a question which is yet to be decided. The main portion of the central tegmental tract appears to come in direct communication with the midbrain in the neighborhood of the third nerve nucleus. Some of its fibers appear to enter and form part of the posterior commissure. The reticular formation (Ref) occupies a large portion of the section but has less of that diffuse appearance so characteristic of it in the apes. Its boundaries are most clearly drawn in the human brain stem.

This level is of particular significance because of its bearing upon the balancing mechanism, in the apparent decrease in prominence of the neural portion of this apparatus.

LEVEL OF THE CEREBELLAR NUCLEI (FIG. 348)

At this level the chief feature is the nuclear development in the medullary substance of the cerebellum. This specialization appears in the extremely complex dentate nucleus (Ndt) which exceeds in its complicated form all other species. The nearest approach to the dentate nucleus in man is that of the gorilla, although both the chimpanzee and orang show a marked increase in complexity of this nuclear structure. In man the nucleus dentatus shows a definite increase in its proportional volume, a greater clearness in definition of its outline, and a much increased richness in its convolutional arrangement. The nucleus emboliformis is somewhat larger in man than in the apes, while the nucleus globosus and nucleus fastigii remain about the same in size as seen in the lower species. Since the dentate nucleus is the final relay station for all neural impulses passing from the cerebellar hemispheres, its expansion seems to follow as a natural consequence of the extension in the lateral lobes. These advances in cerebellar organization denote the increase of coordinative control required by the human musculature in comparison with that of the forms most nearly approaching man in motor capacity.

Such expansion of the cerebellum does not in any way signify a mere extension of power in muscular contraction. Some authorities still attribute to the cerebellum the function of imparting strength to muscular action (the sthenic element in Luciani's cerebellar triad). The arboreal habits of the orang-outang, the chimpanzee and the gorilla call upon the muscular system for the development of great strength. If, as Luciani believed, the cerebellum served in the capacity of augmenting the power of muscular contraction,

FIG. 348. MAN. LEVEL OF THE CEREBELLAR NUCLEI.
CBL, Cerebellum; NDT, Dentate Nucleus; NFG, Nucleus Fastigii; NOD, Uvula; OBL, Oblongata; PY, Pyramid; VEN IV, Fourth Ventricle. [Accession Man. Section N 201. Actual Size 70 × 38 mm.]

then the three great anthropoids should far exceed the human in cerebellar development. Its function more probably is related to the delicate and exact adjustment of the postural attributes which permeate all motor activity. Motion has been described as a fluid stream of postures. The postural element may be discerned in all volitional acts. When investigated in relation to movements of the hand and fingers, the number of postures entering into the simplest acts is found to be surprisingly large. Each of these postures during the entire movement is dependent for its precision upon impulses arising in the cerebellum. This type of cerebellar control applies chiefly to complex motor activities. Disease or injury in the lateral lobes of the cerebellum leads to a condition of ataxia or disarrangement in the performance of such movements. The act is embarrassed by a series of irregular oscillations. Flexion in one place is over-emphasized and must be counteracted by over-extension, which in its turn is extreme. Thus that plastic skeleton of posture about which the execution of each skilled act is molded, loses its cohesive support and has every appearance of thorough disorganization.

The most active agent of skilled performances in man is the hand. Without such specialization as this it would be impossible to develop the range and variety of complex manual movements of which man is capable and for which the vastly increased output of coordinative control becomes necessary. Responding to this demand the lateral cerebellar lobes have shown their expansion. It is not to be overlooked, however, that the lower extremity manifests certain latent potentialities for the development of highly complex acts. Not a few cases are on record in which individuals have been deprived of both upper extremities by amputation at or near the shoulder. Some individuals thus afflicted have so educated the lower extremities and feet as to acquire the control of movements necessary for painting and writing. These movements belong to the group of acquired skilled performances to the usual list of which many others may be added by special training as, for example, those seen in jugglers. The cerebellum thus appears to contain a certain undeveloped potentiality which, under stress of unusual circumstances, may be made available.

LEVEL OF THE INFERIOR PORTION OF THE PONS VAROLII AND THE EMERGENCE OF THE SIXTH CRANIAL NERVE, THE NERVUS ABDUCENS (FIG. 349)

Here the configuration of the section has undergone considerable modification, due to the addition of massive transverse bundles and other structures pertaining to the pons Varolii. By the addition of the pontile elements, the marked distinction between the basis pontis and the tegmentum pontis is clearly established. The boundary line of these two portions is formed by the transversely arranged bundles of the mesial fillet (Mf) through which pass many crossing nerve fibers constituting the trapezoid body,

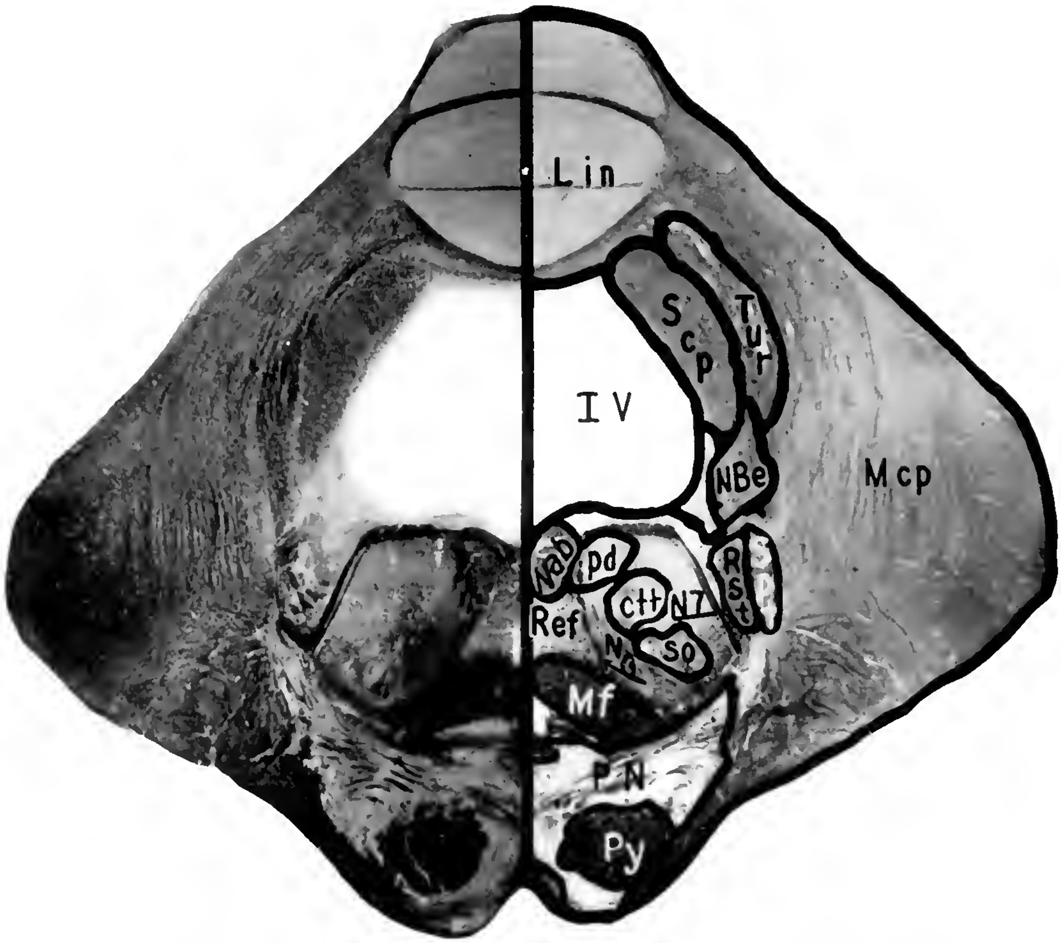


FIG. 349. MAN. LEVEL OF THE INFERIOR PORTION OF THE PONS VAROLII AND THE EMERGENCE OF THE SIXTH CRANIAL NERVE.

CTT, Central Tegmental Tract; LIN, Lingula; MCP, Middle Cerebellar Peduncle; MF, Mesial Fillet; NAB, Abducens Nucleus; NBE, Nucleus of Bechterew; N6, Abducens Nerve; N7, Facial Nerve; PD, Predorsal Bundle; PN, Pontile Nuclei; PY, Pyramid; REF, Reticular Formation; RST, Rubrospinal Tract; SCP, Superior Cerebellar Peduncle; SPT, Spinothalamic Tract; SO, Superior Olive; TUR, Tractus Uncinatus of Russel (Hook Bundle); IV, Fourth Ventricle. [Accession Man. Section C 100. Actual Size 38 × 31 mm.]

a portion of the secondary cochlear pathway. Situated in the lateral extremity of the trapezoid body is the upper pole of the superior olivary body, (SO), a relay station in the pathway of auditory conduction from which some fibers arise to take a course inward and backward in the direction of the nucleus abducentis. These fibers form the peduncle of the superior olivary body. They serve the purpose of transmitting auditory impulses from the superior olive to the nucleus of the sixth nerve, in order that the eyes may be directed toward the source of any sudden sound occurring upon one side or the other of the individual. This pedancle of the superior olivary body develops in all primates, having in man a representation as pronounced as any of the lower forms. Immediate reflex cooperation between ear and eyes is as much a human need for prompt detection of approaching danger as it is essential to the protection of the apes.

The body of the central gray matter, a thin layer forming the floor of the fourth ventricle, is prolonged laterally as a tenuous stratum beneath the subependymal substance over the walls of the ventricular space which now are formed by the massive bundles of the superior and middle cerebellar peduncles. The ventricle itself is somewhat more restricted, due to the fact that it is approaching the caudal orifice of the Sylvian aqueduct. In the ventromesial portion of the central gray matter is the specialized aggregation of nerve cells forming the nucleus abducentis (Nab). This is the nucleus of the sixth nerve which supplies the external rectus muscle of the eye, the fundamental center of all ocular movements in lateral gaze. The emergent fibers of the sixth nerve make their way forward from the nucleus toward the pons Varolii. It is somewhat unusual to observe as in this section three portions of the emergent fibers in the intramedullary course of the seventh nerve which supplies the facial musculature. The microtome was fortunate in revealing the second portion passing along the mesial aspect of the nucleus abducentis, the third portion, the genu facialis, and the fourth portion as the nerve fibers proceed toward the bulbopontile sulcus. The reticular portion of the section is the most extensive region in the tegmentum. The basis contains the elements characteristic of all pontile levels: the stratum superficiale, the stratum complexum in which are the extensive pontile nuclei, the transverse pontile fibers and the fibers of the pyramidal system, and the stratum profundum. In the dorsal area of this field are a few scattered bundles detached from the main pyramidal mass forming the aberrant pyramidal contingents of the pons. The large size of the pontile nuclei is of particular moment, inasmuch as it indicates the accessions in the realm of the cortical organization for skilled acts. These nuclei form one of the main contrasting points between man and apes. The nervus abducens, passing from its nucleus of origin on the floor of the fourth ventricle forward to emerge in the bulbopontile sulcus, is seen in this section as it makes its way through the tegmentum pontis and begins to penetrate the stratum profundum.

LEVEL OF THE MIDDLE OF THE PONS VAROLII (FIG. 350)

At this level a minor alteration has occurred in the configuration of the section which better illustrates the complexity of the pons Varolii and at the same time furnishes means to estimate the size of the superior cerebellar peduncle (Scp). The central gray matter spreads out as a thin layer underlying the floor of the ventricle which is approaching the caudal orifice of the Sylvian aqueduct. At the junction of the floor and the lateral wall is a collection of cells representing the cephalic pole of the nucleus of Bechterew (NBe), part of the vestibular complex. Closely associated with this is a dense bundle of fibers constituting the ascending mesencephalic root of the trigeminal nerve (Tmt). The lateral wall of the ventricular space is formed by the superior cerebellar peduncle (Scp). This peduncle is of interest largely because of its size which, as compared with any of the apes, indicates the augmentation which has occurred in the volume of efferent impulses from the cerebellum, especially from the lateral lobes. In general arrangement the conditions in and about the region of the superior cerebellar

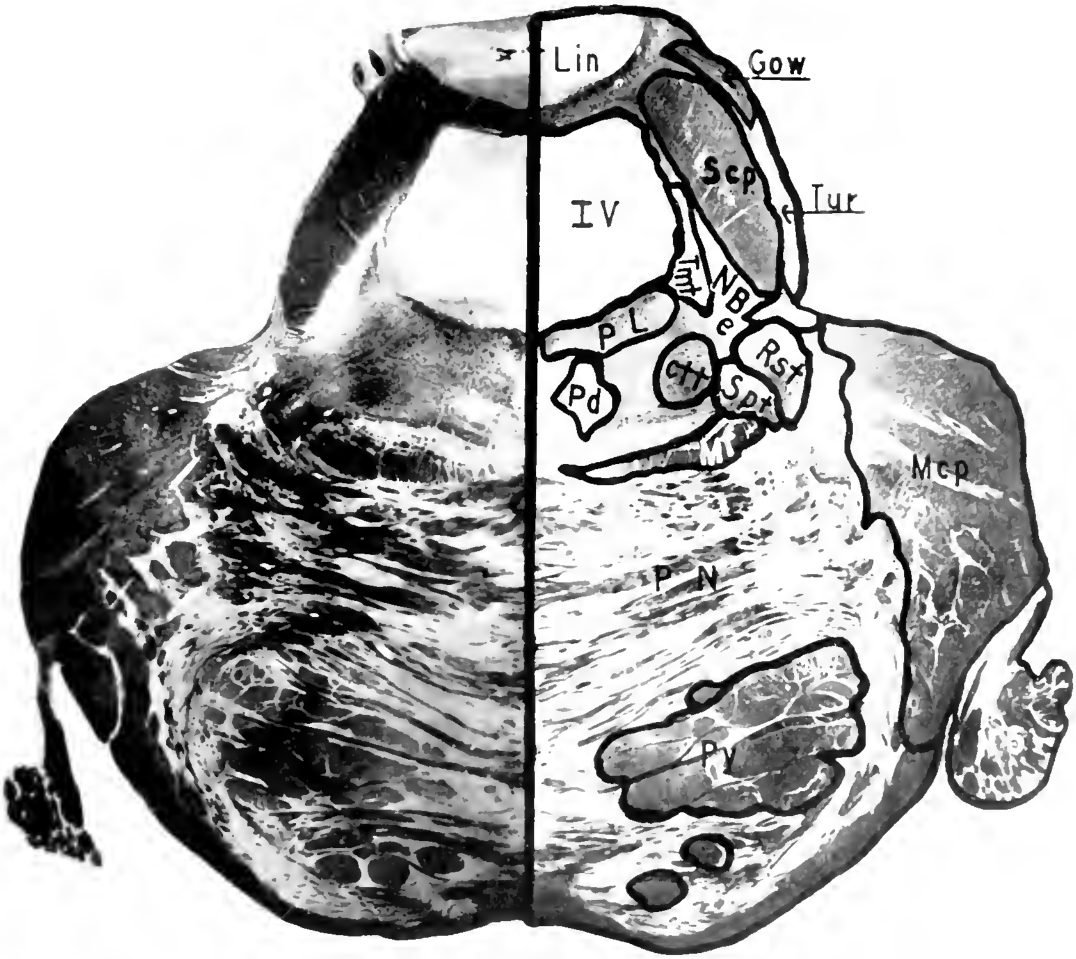


FIG. 350. MAN. LEVEL OF THE MIDDLE OF THE PONS VAROLII.

CTT, Central Tegmental Tract; GOW, Ventral Spinocerebellar Tract; LIN, Lingula; MCP, Middle Cerebellar Peduncle; MF, Mesial Fillet; NBE, Nucleus of Bechterew; N5, Trigeminal Nerve; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PN, Pontile Nuclei; PY, Pyramid; RST, Rubrospinal Tract; SCP, Superior Cerebellar Peduncle; SPT, Spinothalamic Tract; TMT, Tractus Mesencephalici Trigemini; TUR, Tractus Uncinatus of Russel (Hook Bundle), IV, Fourth Ventricle. [Accession Man. Section 715. Actual Size 30 × 26 mm.]

peduncle correspond in minute detail to this area in all of the lower primates. In none of them, however, is the proportion of the superior cerebellar peduncle so great as in man. Judged by this index, it is evident that coordinative control over the muscles has increased in proportion to the acquisition of skilled performances made effective by the human hand. A certain number of fibers from the superior peduncle extend into the roof of the fourth ventricle, and many of them doubtless assume this position to accommodate the increasing volume of this pathway. For the most part, however, those fibers seen in the roofplate belong to the cerebellar commissures.

Lateral to the peduncle is a thin layer of lightly myelinized fibers which constitute the tractus uncinatus of Russel. This fasciculus forms a part of the juxtarestiform body and associates the vermal portions of the cerebellum with nuclear areas in the region of Deiters' nucleus. Lying upon the periphery of the narrow zone forming the tractus uncinatus are the myelinized fibers of the ventral spinocerebellar tract (Gow) pursuing its course to the vermis of the cerebellum. These conditions in the neighborhood of the superior cerebellar peduncle deserve special comment since they maintain an invariable arrangement throughout the primate series. They have varied only in their proportions, the lower forms showing a less highly developed superior cerebellar peduncle and a much more extensive zone corresponding to the tractus uncinatus of Russel. The fibers composing the ventral spinocerebellar tract follow their rather circuitous route to the vermis, maintaining about the same proportions throughout the series. It is difficult to estimate their actual volume, but if anything they may have decreased in man. The increasing size of the superior cerebellar peduncle as contrasted with the relatively decreasing size of the tractus uncinatus produces the variant in the arrangement of this region. Since the uncinate tract of Russel is part of the juxtarestiform body, it represents an activity connected with the intrinsically primitive functions of the cerebellum. Its prominence may well decrease in comparison with the more recent functional accessions of the cerebellum represented by the superior cerebellar peduncle. On the one hand, the uncinate tract denotes organization in the cerebellum related to paleokinesis, particularly concerned in the balancing mechanism, while on the other hand, the superior cerebellar peduncle is an index of developments in coordinative control of precise movements expressing neokinetic specialization.

The outstanding feature at this level is the great increase in the size of the pons Varolii produced by the augmentation of the pontile nuclei. So marked is this expansion that pontile structures of the basis encroach upon the tegmentum pontis to such an extent that some of the pontile nuclei actually lie dorsal to the mesial fillet (P.N., M.f.). Such pontile encroachment may be looked upon as another evidence of the exuberant expansion of these nuclear masses seeking accommodation in all available regions. They appear to extend caudally as a prolongation of the nuclear substance which forms the nucleus arciformis, and to some extent infiltrate the mesial fillet. This invasion of the tegmentum is primarily a human feature. Indications of it may be found here and there in the chimpanzee and in the gorilla, but in the main no such massive extension of nuclear substance into the tegmentum is witnessed in any other species as in man. The basis pontis takes its character much more from these nuclear aggregations than it does even from the great mass of transverse pontile fibers which further increase the actual volume of the pons Varolii. The arrangement of the three layers in the pons is similar to that noted in other species. All of the pontile layers, the stratum superficiale pontis, the stratum complexum pontis and the stratum profundum pontis have their characteristic appearances. The manner in which the transverse fibers accumulate as they approach the lateral aspect of the section to form the middle cerebellar peduncle (M.c.p.) is a feature which has been noted in connection with each form of the primates discussed. In the ventrolateral portion of the section some fibers forming the dorsal roots of the trigeminal nerve (N 5) penetrate the pons. Many of these may be traced inward and backward to a small attenuated mass of gray matter, the cephalic pole of the substantia gelatinosa of Rolando. The reticular formation is clearly bounded but is relatively small in its general proportions and shows no nuclear specializations of note.

In general, the significance of this portion of the stem derives importance from its bearing upon the organization of skilled performances as indicated by the size of the pons Varolii. In particular it denotes an extensive expansion of the neopallium and a marked increase in the volume of those pallio-ponto-cerebellar tracts which afford communication between the cerebral hemispheres and the lateral lobes of the cerebellum.

LEVEL SHOWING THE EMERGENCE OF THE FOURTH OR TROCHLEAR NERVE (FIG. 351)

At this level the contour of the section has undergone those changes incident to the appearance of the caudal orifice of the aqueduct (Aq) and the general approach to the next higher segment of the brain stem. The central gray matter (Cen) entirely surrounds the floor and lateral wall while its roof is formed by a thin layer of the posterior medullary velum. Escaping from the roofplate are the fibers of the trochlear nerve (N 4) which make their way around the lateral aspect of the stem to enter the cavernous sinus in common with the third and sixth cranial nerves. The boundary between the central gray matter and the subjacent reticular formation (Ref) is formed by the posterior longitudinal fasciculus (PL) and the predorsal bundle (PD), as well as the scattered bundles of the fibers constituting the mesencephalic root of the fifth nerve (Tmt). The lateral portion of the tegmental area at this level is occupied by two impor-

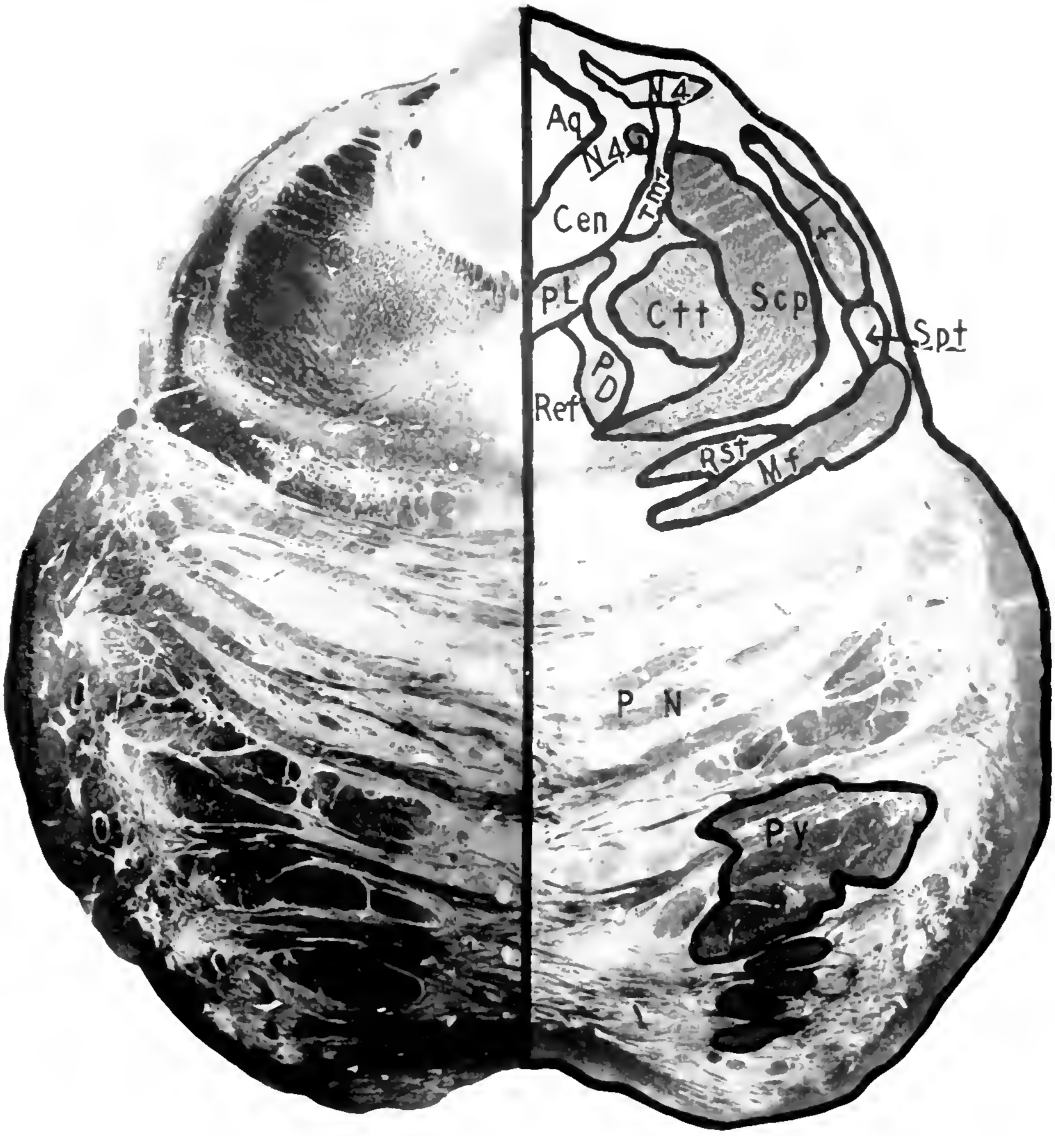


FIG. 351. MAN. LEVEL SHOWING THE EMERGENCE OF THE FOURTH OR TROCHLEAR NERVE.

AQ, Aqueduct of Sylvius; CEN, Central Gray Matter; CTT, Central Tegmental Tract; LL, Lateral Fillet; MF, Mesial Fillet; N4, Trochlear Nerve; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PN, Pontile Nuclei; PY, Pyramid; RET, Reticular Formation; RST, Rubrospinal Tract; SCP, Superior Cerebellar Peduncle; SPT, Spinothalamic Tract; TMT, Tractus Mesencephalici Trigemini. [Accession Man. Section C 458. Actual Size 24 × 24 mm.]

tant systems of conduction fibers. The mesial and more massive is the superior cerebellar peduncle (Scp) in the form of a crescent whose inferior tip is approaching the median line. Lateral to the superior cerebellar peduncle is the lateral fillet (Lf), the secondary pathway in the conduction of auditory impulses. These fibers are approaching a relay station in the inferior colliculus whose elevations are not as yet present at this level. The relative size of the superior cerebellar peduncle is readily appreciated and again affords an opportunity for estimating the volume of efferent impulses passing out of the cerebellum in connection with the function of muscular coordination. The significance of its augmentation has already been discussed and is undoubtedly connected with the vastly increased capacities on the part of man for the finer adjustment in those highly skilled performances which require the finest coordinative control.

The boundary line between the tegmentum and basis in this section is created by the presence of the transversely disposed bundle of fibers of the mesial fillet (Mf). In the basis are all of the elements characteristic of the pons Varolii, including its three major strata, the stratum superficiale pontis, the stratum complexum pontis, containing the large masses of pontile nuclei, and the stratum profundum pontis. The reticular formation (Ref) at this level appears to be reasserting itself as a more extensive structure. At the same time it appears somewhat more diffuse, due to the tendency of the superior cerebellar peduncle to undergo decussation. The formatio reticularis contains no specialized groups of cells at this level. Bordering upon it and perhaps forming a portion of it is a small aggregation of gray matter, the caudal pole of the substantia nigra. This latter structure has been variously interpreted as to its functional significance. At the present time the majority of authorities ascribe to it the regulation of certain automatic associated movements.

LEVEL OF THE INFERIOR COLLICULUS (FIGS. 352, 353)

At this level the midbrain is entered and shows the characteristic modifications occurring in the roofplate. Two symmetrical elevations rise upon either side forming the inferior colliculi (IC). These structures are more conical in shape than is the case in any of the lower primates. From surface appearances these primary way-stations in the pathway of hearing seem to have undergone considerable reduction in the human brain. The significance of such reduction may be gauged by the fact that hearing in man has become much more deliberative in its reactions. Auditory stimuli need and receive more consideration, greater association and more exact evaluation before courses of action are determined in response to them. The need of immediate reflex response as the result of auditory impressions is much less apparent in man than in lower animals. It is probable that such instantaneous reaction as many of the lower apes manifest in consequence of auditory stimuli might prove injurious to man. The adage, "Look before you leap," applies equally to the sense of hearing. Sounds or noises are usually submitted to proper analysis by higher centers in the neural mechanism. Although a certain degree of the ancient stratification still is apparent in the inferior colliculus, reminiscent of its former functional prominence among various parts of the brain, this specialization is but feeble and gives a distinct impression of definite involution. Probably no other single function has undergone more extensive elaboration than the sense of hearing. The evaluation of sounds and the production of speech and music, as well as the associations connected with the many voices of nature, have formed an almost inexhaustible material out of which man has constructed his wealth of auditory perception and understanding. It is little wonder, therefore, that the primitive capitol of hearing has been transferred to a thoroughly modernized neural organization capable of meeting all of the great variety of modification and exigency in the auditory realm.

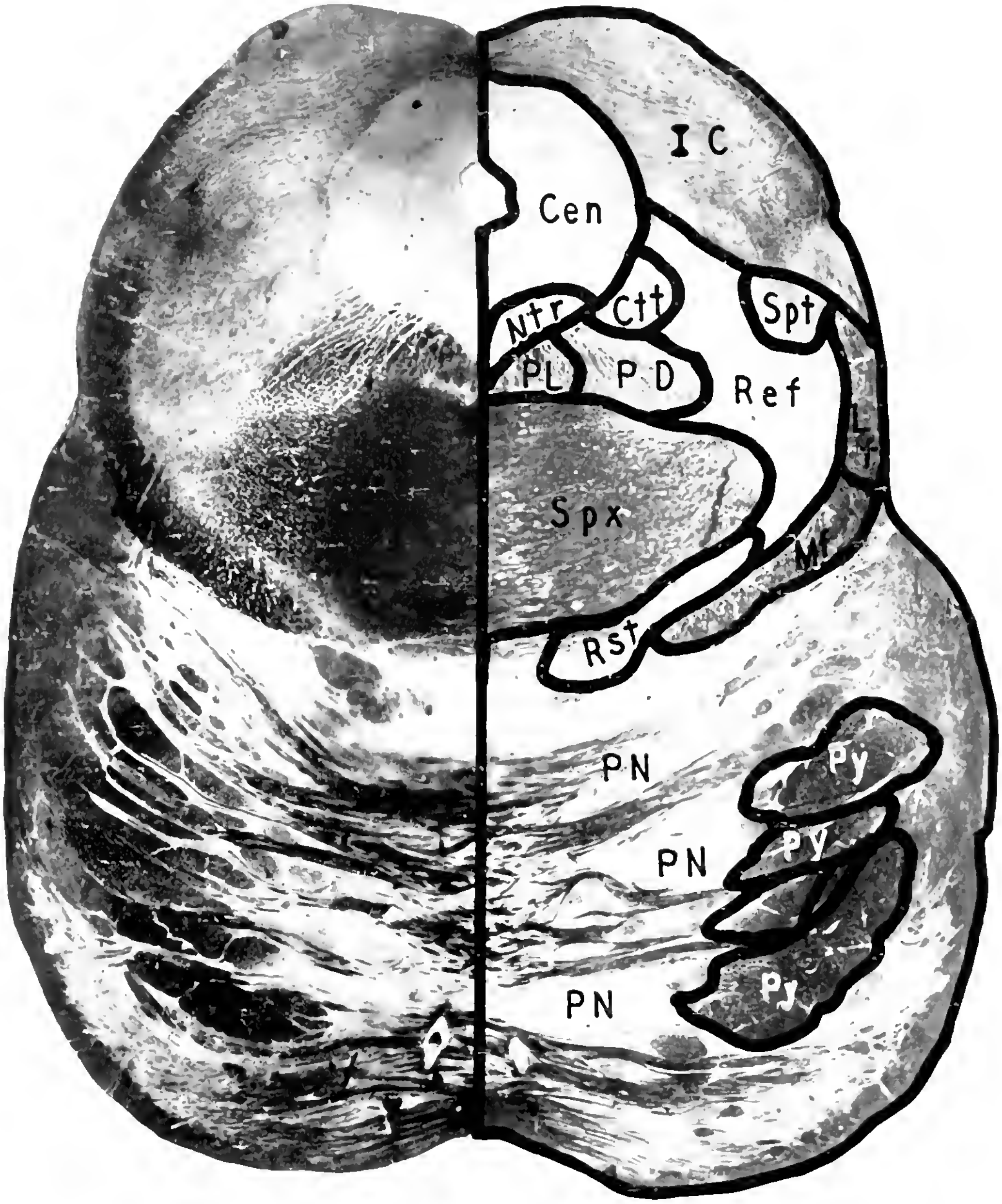


FIG. 352. MAN. LEVEL OF THE INFERIOR COLLICULUS.

CEN, Central Gray Matter; CTT, Central Tegmental Tract; IC, Inferior Colliculus; LF, Lateral Fillet; MF, Mesial Fillet; NTR, Trochlear Nucleus; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; PN, Pontile Nuclei; PY, Pyramid; REF, Reticular Formation; RST, Rubrospinal Tract; SPT, Spinothalamic Tract; SPX, Crossing of the Superior Cerebellar Peduncle. [Accession Man. Section C547. Actual Size 22 × 24 mm.]

The central gray matter (Cen) surrounds the floor and lateral walls of the Sylvian aqueduct, and upon its ventral margin are the extensive bundles constituting the posterior longitudinal fasciculus (PL), the predorsal

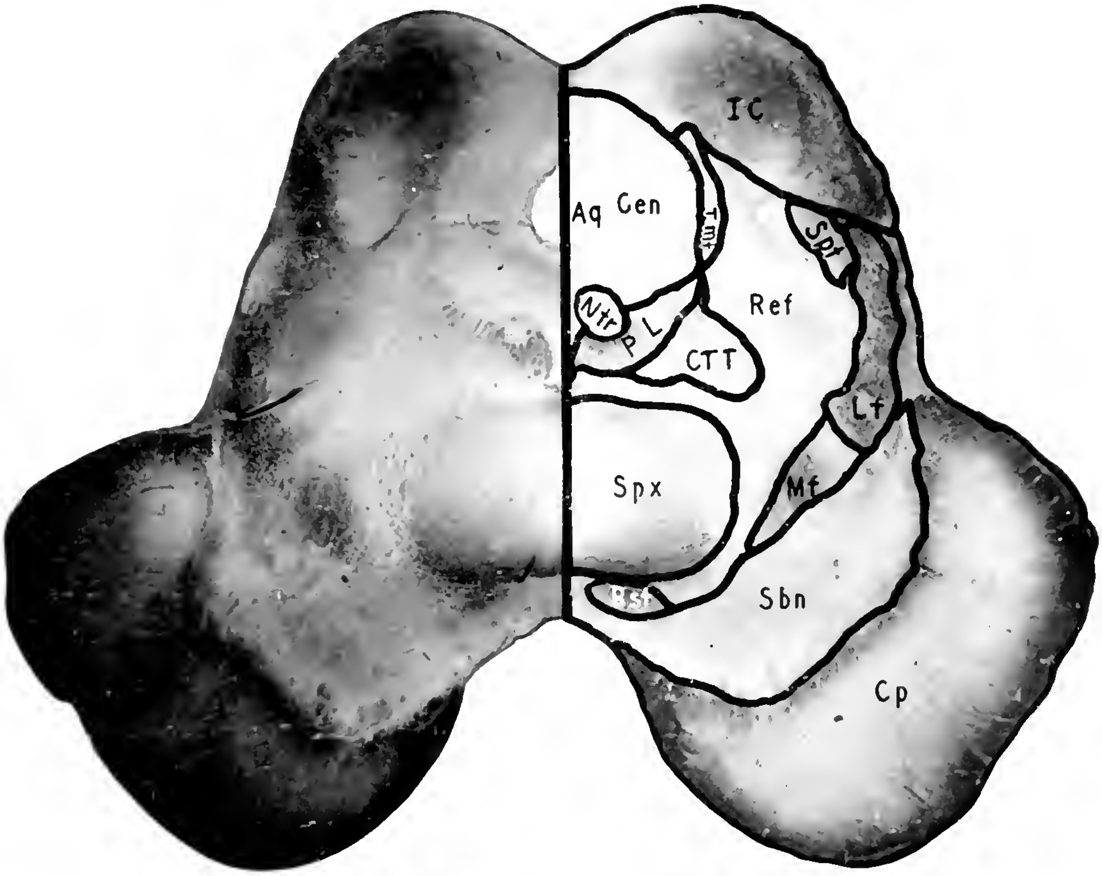


FIG. 353. MAN. LEVEL OF THE INFERIOR COLLICULUS.

AQ, Aqueduct of Sylvius; CEN, Central Gray Matter; CTT, Central Tegmental Tract; CP, Cerebral Peduncle; IC, Inferior Colliculus; LF, Lateral Fillet; MF, Mesial Fillet; NTR, Trochlear Nucleus; PL, Posterior Longitudinal Fasciculus; REF, Reticular Formation; RST, Rubrospinal Tract; SBN, Substantia Nigra; SPT, Spinothalamic Tract; SPX, Crossing of the Superior Cerebellar Peduncle; TMT, Tractus Mesencephalici Trigemini. [Accession Man. Section N918. Actual Size 34 × 19 mm.]

bundle (PD) and some scattered bundles of myelinized fibers forming the mesencephalic root of the fifth nerve (Tmt). The tegmentum itself at this level is further confused by the convergent fibers of the superior cerebellar peduncle (Spx) as they approach their level of decussation. Lateral to the converging peduncle are fibers of the lateral fillet (Lf) entering the inferior colliculus and thus completing the first stage in thepathway of hearing. The mesial fillet (Mf) establishes the boundary between the basis and tegmentum in which former may still be discerned the characteristics of the pons Varolii.

The special feature at this level in all primates is the appearance of the inferior colliculi. That they show some demonstrable diminution in man is indicative of the process of telencephalization which has proceeded throughout the primate series. In man it reaches its termination in that the chief responsibility of the function of hearing has at length been delegated to the cerebral cortex in the region of the temporal lobe.

LEVEL OF THE SUPERIOR COLLICULUS (FIG. 354)

Here the alterations invariably associated with this region of the brain are all apparent. The essential changes are typified by the appearance of two dorsal elevations in the roofplate of the mesencephalon, the superior colliculi (SC). These structures have obviously become much reduced in size as compared with the other primates. They retain but a vestige of their former importance, representing as they do the much reduced optic lobes of the lower vertebrates. Nothing could demonstrate more conclusively the evolutional process which has steadily advanced in the brain than the changes affecting this portion of the stem. In man the process of delegating function from a lower to a higher, more expansible area of the brain is carried to its fullest expression. Although the superior colliculus does manifest a certain degree of stratification in the human brain, although several layers of cells and fibers may be detected in this structure, these are so rudimentary as to leave no doubt that the function of this formerly important region has diminished. The evidence of the inferior and superior colliculi in the midbrain of primates, indicated not by expansion but the reverse, furnishes a convincing record of an evolutional process.

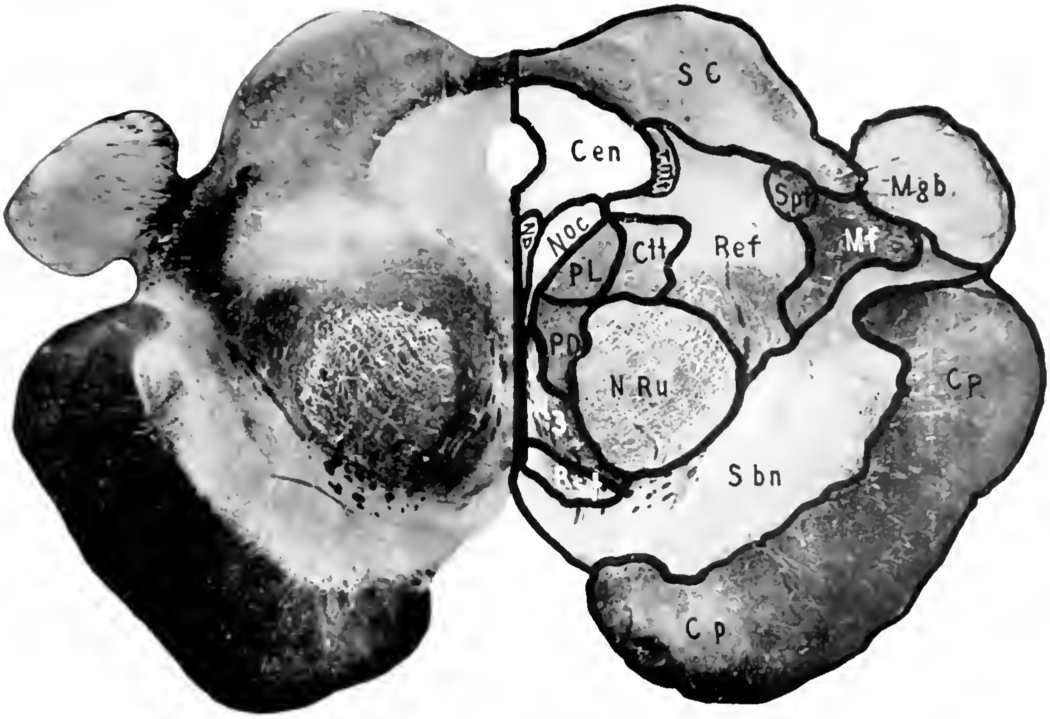


FIG. 354. MAN. LEVEL OF THE SUPERIOR COLLICULUS.

CEN, Central Gray Matter; CP, Cerebral Peduncle; CTT, Central Tegmental Tract; MF, Mesial Fillet; MGB, Mesial Geniculate Body; NOC, Nucleus Oculomotorius; NRU, Nucleus Ruber; N3, Oculomotor Nerve; PD, Predorsal Bundle; PL, Posterior Longitudinal Fasciculus; RET, Reticular Formation; RST, Rubrospinal Tract; SBN, Substantia Nigra; SC, Superior Colliculus; SPT, Spinothalamic Tract; TMT, Tractus Mesencephalici Trigemini. [Accession Man. Section C 647. Actual Size 30 × 14 mm.]

The central gray matter (Cen), which surrounds the aqueduct of Sylvius, in its ventromesial portion contains a large nuclear aggregation, the nucleus oculomotorius (Noc). From this nucleus the nerve fibers arise which supply all of the muscles of the eye with the exception of the external rectus and the superior oblique. The nucleus is noteworthy because of the dense oculomotor decussation and commissural connections. This connection itself is indicative of close internuclear relationship in the interest of stereoscopic vision. The reticular formation (Ref) is now much reduced in size. There has emerged from it a large circular nuclear mass, the nucleus ruber (NRu). This nucleus shows a distinct increase in size compared with the lower and intermediate primates and is even larger than in the great anthropoids. Functionally it serves as a relay in the transmission of impulses mainly arising in the lateral lobes of the cerebellum. It may also be the case that some fibers from the cerebellum are relayed in this nucleus to pass cephalad into the interbrain or even the endbrain. The marked increase of the nucleus in the human brain is important as bearing upon the increment in coordinative control already indicated in the size of the lateral lobes of the cerebellum.

Ventral to the reticular formation is a massive aggregation of nuclear substance, the substantia nigra (Sbn). Whatever may be the final opinion concerning the functional significance of this large mass of gray matter in the midbrain, it unquestionably manifests a progressive increase in size and definition in the primates. Ventral to the substantia nigra is the collection of fibers constituting the cerebral peduncle (CP). These peduncular fibers provide for all those intricacies of motor activity essential to the life of the hunter in the use and the contrivance of his weapons and implements. They serve the expression of man's abilities as agriculturalist, home-builder, artisan and artist. Without these connections none of the activities characteristic of human society and cultural organization would be possible. It may be questioned, therefore, why these structures, denoting such preeminent achievements in man, have any representation whatsoever in apes and lower mammals. It is, however, not the mere presence of these neokinetic fibers represented in the cerebral peduncle which gives them their significance. They have a long mammalian history, in which their final expansion in the human brain displays this critical surplus over and above their primitive, fundamental development.

Lateral to the reticular formation and apparently emerging from it is a large protuberance, the mesial geniculate body (Mgb) connected with the pathway of hearing. It appears to increase progressively in size through

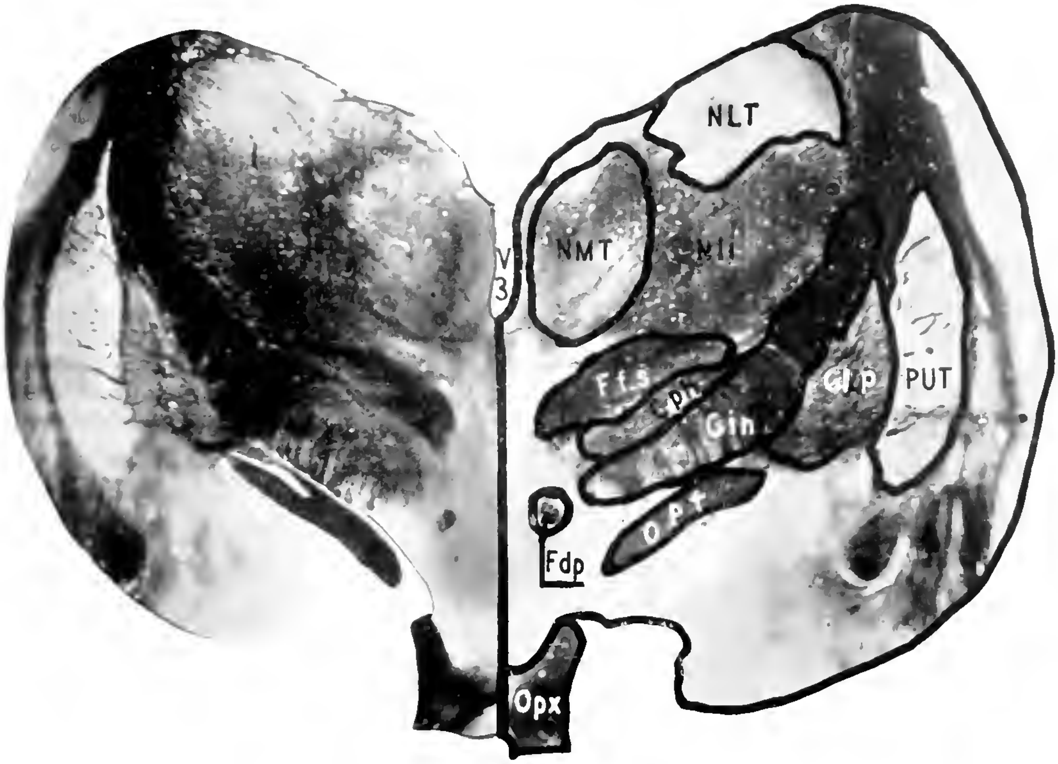


FIG. 355. MAN. LEVEL OF THE OPTIC CHIASM.

CIN, Internal Capsule; CPH, Corpus Hypothalamicum; FDP, Descending Pillars of the Fornix; FFS, Fields of Forel; GLP, Globus Pallidus; NLT, Lateral Nucleus of the Thalamus; NMT, Mesial Nucleus of the Thalamus; NIL, Internal Lateral Nucleus of the Thalamus; OPT, Optic Tract; OPX, Optic Chiasm; PUT, Putamen; V3, Third Ventricle. [Accession Man. Section C 790. Actual Size 64 × 29 mm.]

the primate series and in man has larger dimensions than in any of the apes. Between the two peduncles is a wide optico-peduncular space which contains the mammillary bodies, the postinfundibular eminence, the attachment of the infundibular stalk and the tuber cinereum. All of these are more prominent than the corresponding structures in lower primate brains. The intercollicular sulcus between the superior colliculi is broader and deeper than in the anthropoids. It forms a larger pineal fossa for the epiphysis cerebri. The function attributed to the epiphysis in inhibiting growth and

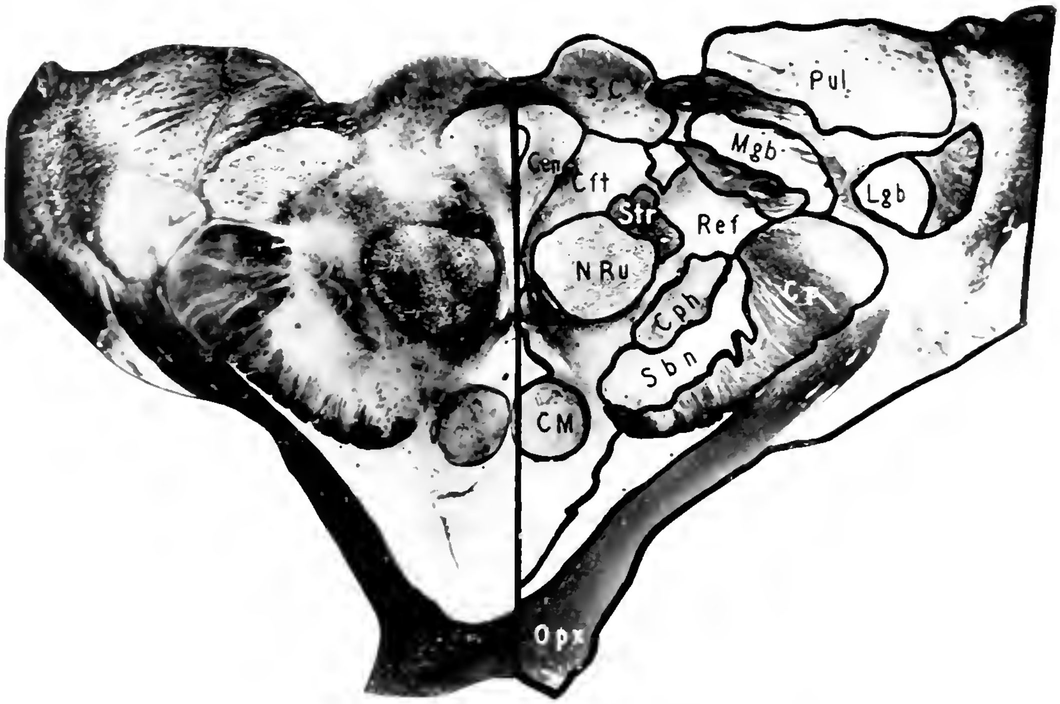


FIG. 356. MAN. LEVEL OF THE OPTIC CHIASM.

CEN, Central Gray Matter; CM, Mammillary Body; CP, Cerebral Peduncle; CPH, Corpus Hypothalamicum; CFT, Central Tegmental Tract; LGB, Lateral Geniculate Body; MGB, Mesial Geniculate Body; NRU, Nucleus Ruber; OPX, Optic Chiasm; PUL, Pulvinar; REF, Reticular Formation; SBN, Substantia Nigra; SC, Superior Colliculus; STR, Striatorubral Tract. [Accession Man. Section 980. Actual Size 65 × 35 mm.]

retarding sexual development is significant in that it delays maturity in man to a much later period than in other mammals.

LEVEL OF THE OPTIC CHIASM (FIGS. 355, 356)

At this level the contour of the section shows the characteristic modifications of transition from the midbrain to the interbrain. The third ventricle (V3) appears as a deep narrow cleft between the two nuclear structures which form the optic thalami. In the most ventral position and forming the floor of the ventricle at this level is the optic chiasm (Opx) into which enter the optic nerves and from which the optic tracts depart on

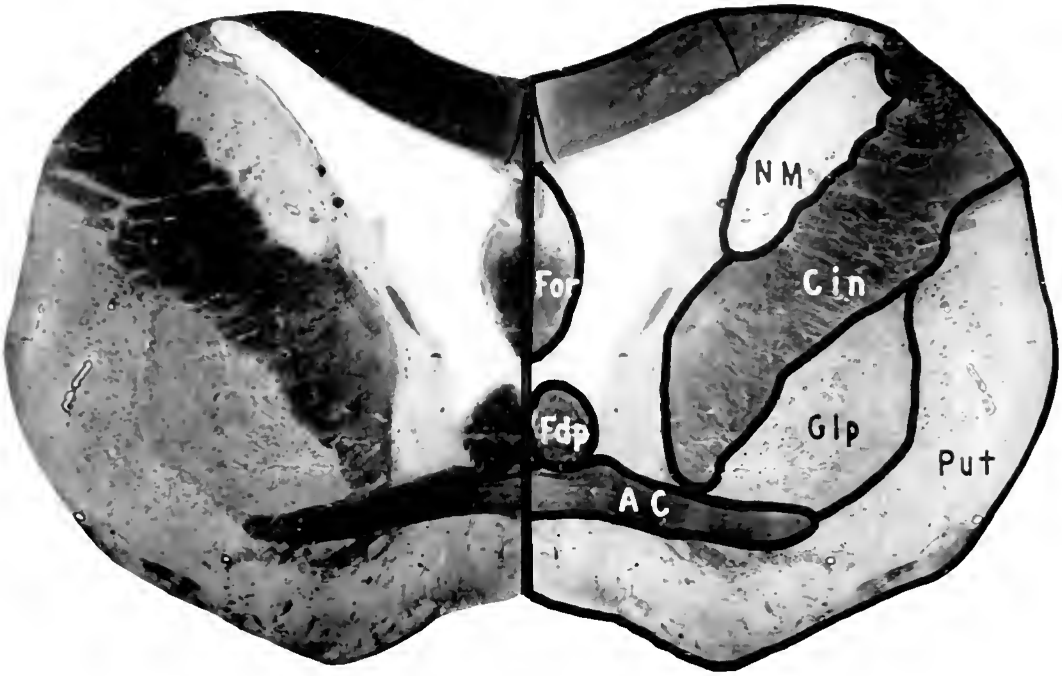


FIG. 357. MAN. LEVEL OF THE ANTERIOR COMMISSURE.

AC, Anterior Commissure; CIN, Internal Capsule; FDP, Descending Pillars of the Fornix; FOR, Fornix; GLP, Globus Pallidus; NM, Nucleus Masticatorius; PUT, Putamen. [Accession Man. Section N 1052. Actual Size 63 × 20 mm.]

their way to the several relay stations before they end in the occipital lobe. The third ventricle is divided into a dorsal and a ventral division by the interposition of the commissura mollis. The thalamus is contiguous with a dense bundle of fibers constituting the internal capsule (Cin) which represents the cephalic continuation of the cerebral peduncles. The capsule is placed between the ventrolateral surface of the thalamus and the mesial surface of the corpus striatum which in this section presents the two major portions of the lenticular nucleus, the globus pallidus (Glp) and the putamen

(Put). Other morphological features of this level are indicated by corresponding markings which appear in the legends accompanying the figures.

LEVEL OF THE ANTERIOR COMMISSURE (FIG. 357)

Here the brain stem comes to its cephalic termination. The third ventricle, less deep and somewhat broader than in the level of the optic chiasm, is flanked upon either side by the cephalic extremity of the optic thalamus. All of the structures in this region of the brain in man correspond in detail with the homologous elements of the lower and intermediate primates as well as the great anthropoids.

Features of Human Brain Showing Greatest Evolutional Significance

In concluding the review of the human brain, it is difficult to decide which features have the greatest evolutional significance. The neopallium, pons Varolii, pyramid and cerebral peduncle probably should be given the place of first importance. The lateral lobes of the cerebellum, the dentate and red nuclei, the superior cerebellar peduncle and inferior olive are but little less decisive in their evidence. All of these structures are essential factors in the organization and control of mammalian motor specialization. Their progressive evolutionary development in the primates denotes to what degree behavioral capacity has been extended. The history of these structures is closely interwoven with the differentiation of the extremities and their record reveals how that process has advanced through many phases from apes to man until the human hand made its appearance. This specialization is the final test which may be employed to explain the extensive developments of the human brain.

Chapter XXVI

RECONSTRUCTION OF THE GRAY MATTER IN THE HUMAN BRAIN STEM

THE reconstruction of the gray matter in the human brain stem reveals those modifications, expansions and elaborations which represent the culmination of the evolutional process traced through the primate order. Certain features made more evident by this method of visualization deserve particular consideration. In this regard, attention first directs itself to the pontile nuclei, the greatest mass formed by any one specialized structure contributing to the composition of the neuraxial gray matter. This imposing nuclear collection in man contributes a greater proportional amount of gray matter to the make-up of the brain stem than it does in any of the lower members of the primate group. Not only is this development easily recognized in the actual amount of nuclear material but also in the complicated disposition of the fibers which arise within it, and coursing through the nuclear matrix break it up into a more intricate nuclear mass than is seen in any of the other representatives of this series.

Another impressive mass of gray matter is the arciform nucleus, which represents a marked advance over that seen in the lower forms, consisting of a layer of gray matter almost completely enveloping the ventral surface of the infrapontile portion of the brain stem. The inferior olivary complex also reaches a degree of complication considerably in advance of that hitherto observed in the phylum, while the colliculi show the final steps in the process which has already been observed to be in progress, the inferior colliculus continuing to show a steady reduction in size and complexity, while the superior colliculus barely holds its own in comparative and absolute differentiation.

One other feature which at once attracts attention in this general survey of the exposed nuclear material is the comparative decrease in the size and importance of the reticular formation, the matrix out of which has developed the great majority of the nuclear masses belonging to the gray matter of the brain stem. The reconstruction in general does not give the impression of massiveness which might be expected in this the largest brain stem of the series. The nuclear accumulations, although increased relatively in size, differ materially from those which have been observed in the lower members of the series in an increasing sharpness of definition, a greater degree of delicacy and clearness of outline, which serves more sharply to differentiate them from those of the lower primates than does any material increase in bulk or size. The fundamental structures of the brain stem, the reticular formation, the nuclei of the cranial nerves and the specialized masses of gray matter in the region of the mesencephalon, particularly the nucleus ruber and the substantia nigra, do not present any material alteration in the appearance of these structures as they have been observed in the lower orders in this series.

The organized masses which have materially changed in size, complexity and in contour are those connected with the functions which in man have achieved a greater degree of integration and coordination than that attained by any of the lower members of the primate group. This particularly applies to the pontile nucleus which develops, pari passu, with the expansion of the cerebral hemispheres and organization of synergy, the contribution of the cerebellum to animal motion. The olivary nucleus which must be considered as a comparative newcomer in the organization of the brain stem, as it presents material complexity only in the upper primates, shows a marked advance in man over that which has been observed in the other members of this group. Although its function is not fully understood, its development has been steady, definite and continued. The conclusion here advanced may not yet be entirely supported by definite evidence, nevertheless the increase in complexity and size of the olive has paralleled the emergence of the hand as an independent member for the exploration of the environment. This improvement in manual dexterity in conjunction with the perfection of binocular

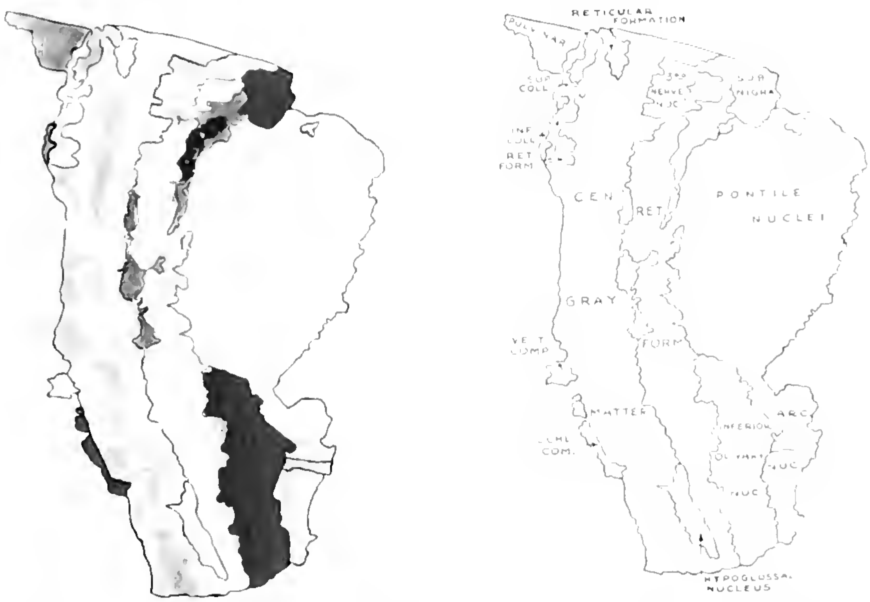


FIG. 358. LATERAL SURFACE OF GRAY MATTER OF BRAIN STEM, HOMO SAPIENS. KEY TO DIAGRAM. ARC. NUC., Arciform Nucleus; CEN. GRAY MATTER, Central Gray Matter; COCHL. COM. Cochlear Complex; INF. COLL., Inferior Colliculus; INFERIOR OLIVARY NUC., Inferior Olivary Nucleus; RET. FORM., Reticular Formation; SUB. NIGRA, Substantia Nigra; SUP. COLL., Superior Colliculus; VEST. COMP., Vestibular Complex; 3RD NERVE NUC., Nucleus of the Oculomotor Nerve.

vision may be explained by the critical exercise of the visual function in the guidance of the hand and arm. One other feature which deserves mention is the marked increase in the clearness and definition evinced by the various channels, which the long white fiber tracts have produced through the reticular formation and the other portions of the gray matter of the stem. These channels present a greater sharpness and definition of outline than that seen in the preceding members of this group.

The Dorsal Medullary Nuclei

In the lowest part of the reconstruction the dorsal medullary nuclei appear already fairly well developed. The nucleus of the column of Goll, situated mesially, possesses the large overhanging lateral extension which is characteristic of the dorsal nuclear accumulations. This lateral extension of the nucleus extends outward and almost hides from view the more laterally placed nucleus of the column of Burdach. The nucleus of Goll continues upward enclosed by a dwindling mantle of fibers and containing within its lateral concavity a considerable bundle of fibers of the column of Goll. As it approaches the opening of the fourth ventricle it presents a slight lateral deviation produced by the widening of the ventricular system in this locality which has been so characteristic of the behavior of these structures in the forms already described. The nucleus does not, however, participate in the formation of the lateral wall of the fourth ventricle, being at all times excluded from that cavity by the circumventricular mantle or lining of subependymal gray matter. The nucleus gradually diminishes in size as the ascending fibers reach their cells of termination, and it finally disappears at a level only slightly higher than the point of opening of the fourth ventricle. In appearance the nucleus is more or less solid and is not broken up into any definite arborization by the fibers composing the tract which lie grouped together in the concavity formed by the lateral overhang of the nucleus.

The nucleus of the column of Burdach appears at a slightly higher level than the preceding nucleus, as a rounded elevation on the dorsal surface of the central gray matter at about the junction of the body with the lateral horn. It rapidly extends dorsally, the base widening while its dorsal termination gradually moves laterally in conformity with the deviation shown by the preceding nucleus. It also develops a lateral overhanging mass of gray matter enveloped by a steadily diminishing number of fibers, and in the lateral concavity of the overhanging portion of the nucleus and almost surrounded by it appears a distinct bundle of the remaining fibers of the ascending tract of Burdach. The nucleus continues to increase in size until it reaches the level at which the nucleus of Goll begins to diminish and then it rather rapidly decreases in size and importance, its place being taken by the appearance of the nuclear material appearing in connection with the vestibular complex. In association with the upper half of the nucleus there develops upon

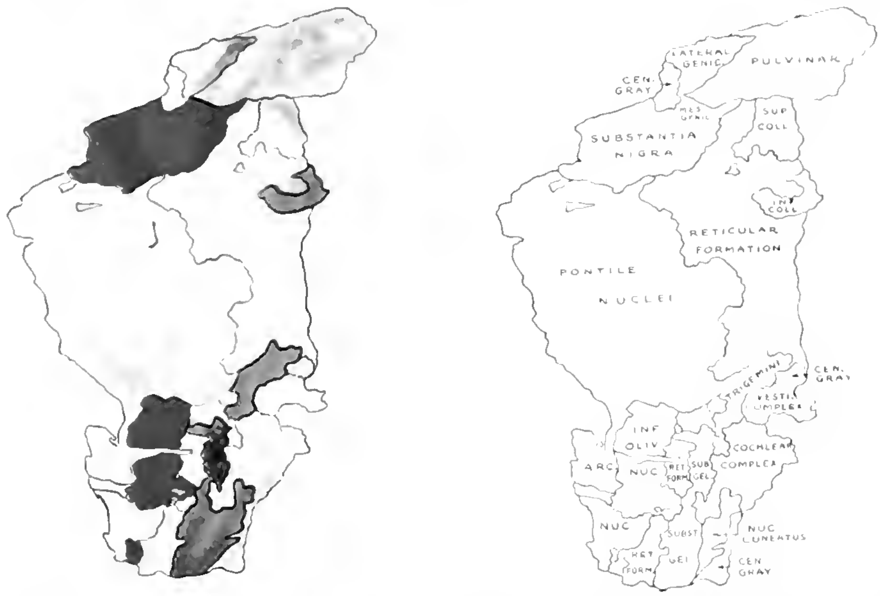


FIG. 359. LATERAL SURFACE OF GRAY MATTER OF BRAIN STEM, HOMO SAPIENS.

KEY TO DIAGRAM. ARC. NUC., Arciform Nucleus; CEN. GRAY, Central Gray Matter; INF. COLL., Inferior Colliculus; INF. OLIV., Inferior Olivary Nucleus; LATERAL GENIC., Lateral Geniculate Body; MES. GENIC., Mesial Geniculate Body; NUC. CUNEATUS, Nucleus Cuneatus; RET. FORM., Reticular Formation; SUB. GEL., SUBST. GEL. and TRIGEMINI, Substantia Gelatinosa Trigemini; SUP. COLL., Superior Colliculus; VESTI. COMPLEX, Vestibular Complex.

its lateral aspect a mass of gray matter, the nucleus of Blumenau, apparently connected with the nucleus of Burdach.

The substantia gelatinosa Rolandi is continued upward into the oblongata as the receptive nucleus for the trigeminal nerve, being called in this region the substantia gelatinosa trigemini. The nucleus is somewhat more extensive both above and below and presents a definite constriction in the region of the entry of the cochlear division of the eighth nerve. This has been mentioned previously and may be called the waist of the trigeminal nucleus. It maintains a relatively unchanged position in its course upward through the brain stem, lying almost in the lateral meridian, and is influenced but little by the lateral deviation which is so definitely present in the change of position of the dorsal medullary nuclei. The nucleus presents a few lateral extensions which proceed outward between the descending trigeminal fibers particularly in the region where the nucleus of Blumenau appears, and it is difficult to determine whether the latter belongs to the trigeminal complex or to the nucleus of the column of Burdach. At the level of the entrance of the cochlear division of the eighth nerve, the substantia gelatinosa trigemini undergoes a definite diminution in size, recedes from the surface of the stem, then gradually increasing in size it becomes flattened and applied to the lateral surface of the reticular formation. As the nucleus continues upward it finally presents a dorsomesial inclination and disappears within the reticular formation, being covered on its lateral aspect by a prolongation of this nuclear matrix which envelops it on its ventral, lateral and finally on its dorsal aspect. The disappearance of the substantia gelatinosa trigemini from the surface of the reconstruction takes place above the upper limit of the vestibular nuclei.

The Inferior Olivary Nucleus

The inferior olivary nucleus appears in the lowest portion of the reconstruction as a narrow, flattened lamina of gray matter disposed in an oblique direction dorsomesially from the ventrolateral angle of the reconstruction and pointing toward the central gray matter. As this lamina, which is the ventral accessory olivary nucleus, is followed upward there begin to appear masses of gray matter in connection with it, dorsal to its mesial extremity. These represent the first appearance of the dorsal accessory olivary nucleus. As the ventral accessory nucleus is traced further it presents numerous irregularities in size and shape and proceeds upward in a relatively constant position, connected at its mesial extremity by a discontinuous series of nuclear bridges with the dorsal accessory nucleus. It comes to an end at about the junction of the upper and middle thirds of the olivary complex, slightly caudal to the first appearance of the pontile nuclei and the termination of the arciform nucleus. The dorsal accessory olive seems definitely to give rise to the main

FIG. 360. DORSAL SURFACE OF GRAY MATTER OF BRAIN STEM, HOMO SAPIENS.
Key to Diagram. cen. gray matter, Central Gray Matter; lat. genic. body, Lateral Geniculate Body; mesial genic. body, Mesial Geniculate Body; nuc. clav., Nucleus Clava; nuc. cun., Nucleus Cuneatus; pont. nuc., Pontile Nucleus; ret. form., Reticular Formation; zona inc., Zona Incerta.

mass of the olivary nucleus, this sac-like structure apparently developing from the lateral extremity or ventral surface of the dorsal accessory nucleus.

The main mass of the inferior olivary nucleus forms a plicated sac, the mouth of which is directed dorsomesially, while the fundus, which is directed ventrolaterally, presents numerous convolutions producing the eminence on the surface of the stem, called the olivary eminence. Dorsomesially, the dorsal lamina of the olivary nucleus and the dorsal accessory nucleus fuse and rest upon the ventral surface of the reticular formation which is hollowed out to receive this mass of gray material. The inferior olivary nucleus proper appears slightly above the point of opening of the fourth ventricle, increases rapidly in size both ventrodorsally and mesiolaterally, and continues upward as a prominent mass of gray matter. Above the point at which the pontile nuclei are first seen the accessory portions of the nucleus disappear and the nucleus itself contracts, producing a dome-shaped structure which lies within the more superficially placed masses of gray matter representing the caudal portion of the pontile nuclei. Laterally the mass of the inferior olivary nucleus is separated from the ventral surface of the reticular formation by a considerable space which is occupied by the continuation upward of the lateral white column of the spinal cord.

The Reticular Formation

This mass of nuclear material representing the matrix from which many specialized nuclei have differentiated does not bulk so largely nor attain the apparent importance which it manifests in the lower members of the series. It appears as a more or less quadrilateral mass of gray matter extending obliquely from the ventrolateral angle of the oblongata, dorsomesially to its point of confluence with the body of the gray matter and at a higher level the floor of the fourth ventricle. Its ventromesial surface is more or less irregular, presenting a concavity at the point where the inferior olivary nucleus comes into close relationship with the reticular formation. In the lower portion of the oblongata it is separated from its fellow of the opposite side by a considerable distance which is occupied by the longitudinally coursing groups of medianly disposed fibers. As these structures gradually seek other positions in the brain stem the reticular formation approaches the midline and its dorsomesial extremity becomes wider and flatter as it comes into contact with the raphe. In the lowest portion of the reconstruction the ventrolateral extremity of the reticular formation is continued ventrally and laterally into two prolongations, the ventral one of which is continuous with the cephalic extremity of the ventral gray column of the spinal cord, while the dorsal extension becomes thin and concave dorsally to receive the ventral surface of the substantia gelatinosa trigemini. As these prolongations are

FIG. 361. VENTRAL SURFACE OF GRAY MATTER OF BRAIN STEM, HOMO SAPIENS.
KEY TO DIAGRAM. CEN. GRAY MATTER, Central Gray Matter; HYP. NUC., Hypoglossal Nucleus; N3 NUC., Oculomotor Nucleus; SUPERIOR OLIVARY NUC., Superior Olivary Nucleus; ZON. INC., Zona Incerta.

traced upward the ventral extension diminishes in size and finally disappears, leaving only the upward continuation of the dorsal prolongation lying in close contact with the substantia gelatinosa trigemini. This thickens somewhat, becomes irregular and then fenestrated by bundles of white fibers. The reticular formation finally becomes disposed as an irregular, more or less transverse mass of gray matter in close contact dorsally with the subependymal gray matter of the floor of the fourth ventricle in which may be found channels produced by the longitudinal and transversely crossing bundles of fibers and containing many more or less well-defined nuclear accumulations, the remainder of the mass appearing as an indiscriminate, undifferentiated nuclear matrix.

The dorsal surface of the reticular formation comes into intimate relationship with, and its conformation is greatly influenced by the substantia gelatinosa trigemini, the floor of the fourth ventricle, and the numerous nuclear collections which appear in this vicinity in connection with the origin and termination of many of the cranial nerves. In the lower part of the pons the reticular formation is much reduced in thickness, the deep layer of the pontile nucleus being separated from the floor of the fourth ventricle by only a small amount of reticular formation. In this region the fibers underlying the floor of the ventricle form a considerable condensation limiting the dorsal extent of the reticular formation and reduce the gray reticular formation to a body of relatively small dimensions. In the mid-portion of the pontile tegmentum, however, the reticular formation increases in thickness and is disposed as a more or less transverse quadrilateral mass presenting a smooth median surface almost in direct contact with the raphe. The development in this region of the trapezoid body and the lateral fillet serves to differentiate the more mesial portion of the reticular formation into a thicker dorsal subdivision in contact with, or separated by only a small amount of white matter from, the floor of the fourth ventricle, and a thin lamina of gray matter which develops ventrally in contact with the pontile nucleus. Laterally in the mid-portion of the pons, these two subdivisions of the reticular formation join, the point of junction corresponding to the lateral extremity of the floor of the fourth ventricle.

Still further laterally a thin edge of the reticular formation works outward and backward, insinuating itself between the surface of the brain stem and the superior cerebellar peduncle, which as it leaves the roof of the fourth ventricle turns forward, upward and inward in a spiral course toward the red nucleus of the opposite side which is situated in the ventral portion of the mesencephalic tegmentum. This channel formed by the superior cerebellar peduncle is large, well defined and distinct. It is limited mesially by that portion of the reticular formation which is in contact with the floor of the fourth ventricle, and the aqueduct of Sylvius, while laterally it is first uncovered by the reticular formation but as it sinks deeper and deeper into the tegmentum it is gradually surrounded by the thin lateral extensions of the reticular formation already mentioned. As the superior cerebellar peduncle penetrates the tegmentum and moves mesially and ventrally it progressively reduces the amount of reticular formation between it, the floor of the fourth ventricle and the median raphe, until in the upper portion of the metencephalon the peduncle reaches the midline and completely obliterates that part of the reticular formation which lies mesial to it. In this region the reticular formation is divided by the superior cerebellar peduncle into two portions, a thin lamina ventrally which has already been mentioned as being in contact with the deep layer of the pontile nucleus and a dorsomesial triangular mass concave laterally which rests mesially on the raphe and dorsally on the ventricular gray matter. The ventrolateral lamina of the reticular formation fuses dorsally with the dorsomesial triangular mass at the dorsolateral angle of the brain stem at the level of the upper portion of the fourth ventricle and the beginning of the aqueduct of Sylvius. As the superior cerebellar peduncle moves ventromesially toward its decussation this area of fusion between the ventrolateral lamina and the dorsomesial mass of the reticular formation becomes more massive.

In this vicinity a second tunnelling of this portion of the reticular formation takes place by the course of the lateral fillet from the ventrolateral angle of the brain stem as this structure approaches the inferior colliculus. The reticular formation lying immediately subjacent to the inferior colliculus assumes considerable proportions and forms a foundation or support for this colliculus at its ventrolateral extremity. This lateral mass of the reticular formation continues upward and forms a base also for the superior colliculus, while between the inferior and superior colliculi a dorsal extension of the reticular formation passes around the dorsal surface of the brain stem to end by meeting its fellow of the opposite side at the midline, thus completely surrounding the central gray matter of the mesencephalon. At the cephalolateral extremity of the inferior colliculus the reticular formation is tunnelled obliquely ventrad, cephalad and somewhat laterad by the course of the inferior brachium which connects the inferior colliculus with the mesial geniculate body. This channel lies partly on the surface but at times it is bridged by extensions of the reticular formation which pass ventrally from the portion lying immediately beneath the superior colliculus, and dorsally from the part of the reticular formation forming the ventral lip of the groove.

Above the point at which the superior cerebellar peduncle decussates, the reticular formation adjacent to the raphe gradually increases in amount ventrally and laterally until it completely surrounds the decussated superior cerebellar peduncle which is now terminating in the red nucleus and forming a part of its capsule. This portion of the reticular formation surrounding the red nucleus and its capsule is continued upward through the mesencephalon and becomes continuous with the zona incerta of the diencephalon. In the upper pontile and lower mesencephalic region the reticular formation forming the ventral lip of the channel containing the inferior brachium is continued upward as a lateral support for the substantia nigra. In the mesencephalon, as the lateral portion of the reticular formation is passing upward to fuse with the zona incerta of the diencephalon, it sends out a lateral extension which passes dorsal to the substantia nigra and ventral to the mesial geniculate body, thus separating these two structures. This extension of the reticular formation is curved ventrally into the angle between the mesial geniculate body and the mesial portion of the diencephalon to a narrow, tapering point.

The more mesial reticular mass continues upward in rather an irregular form and fuses with the reticular formation of the diencephalon, gradually giving place to the mesial group of thalamic nuclei.

The Arciform and Pontile Nuclei

The arciform nucleus consists of a thin lamina of gray matter lying directly ventral to the pyramidal tract and beneath the surface of the brain stem. It consists of an irregular gray lamina which in various parts of its course sends prolongations laterally around the ventrolateral surface of the stem. It increases rather rapidly in width until it reaches the mid-olivary region where it achieves its greatest lateral expansion, the lateral limit of this extension being the *postolivary sulcus*. From this point the arciform nucleus rapidly diminishes in size and comes to a termination slightly caudal to the origin of the pontile nucleus. The arciform nucleus extends mesially around the pyramidal tract at some points into the ventromesial sulcus of the brain stem, but in the greater portion of its extent it stops short of the ventromedian sulcus. Its dorsal surface corresponds accurately with the conformation of the pyramidal tract which immediately underlies it, and at its lateral extremity it approaches the fundus of the inferior olivary nucleus and also further dorsally comes into direct relationship with the reticular formation.

The pontile nucleus first appears at about the middle of the main olivary nucleus at a level slightly above the termination of the arciform nucleus, as a small collection of gray matter situated mesial to the pyramidal tract. It continues upward in this position, steadily extending laterally both ventral and dorsal to the pyramidal tract to which it is closely applied, until the upper limit of the inferior olivary nucleus is reached. From this point the pontile nucleus increases very rapidly in size and complexity, becoming complete mesially and surrounding the pyramidal tract ventrally, mesially and dorsally with an unbroken sheath of nuclear material. The pyramidal tract laterally still remains uncovered and is situated between the ventral surface of the inferior olivary nucleus and the lateral extremity of the ventral lamina of the pontile nucleus. The pontile nucleus continues to increase in size and sends a prolongation around the uncovered lateral surface of the pyramidal tract which, fusing with the already established deep layer of the pontile nucleus, now forms a complete investment for the pyramidal tract. The pontile nucleus in this region is divided into a massive structure ventrally and a somewhat more reticulated collection of gray matter dorsally, which begins to show channels through which stream the decussating fibers of the middle cerebellar peduncle. The massive character of the ventral layer of the pontile nucleus gradually loosens and becomes broken up into a vastly reticulated series of laminae of gray matter separated by transversely crossing pontile fibers.

As the nucleus assumes greater proportions, it may be seen to form three divisions, a ventral circumferential layer which is quite smooth and relatively unbroken ventrally, a deep transverse layer in contact with the tegmentum, and an intermediate lace-like arrangement of nuclear material. The surface layer of the pontile nucleus, the stratum superficiale pontis, conforms to the contour of the middle cerebellar peduncle, while the deep layer, the stratum profundum pontis, is in direct contact with the tegmentum. Between these two rather definite laminae may be seen disposed in a very irregular branching manner many other layers of gray matter, the stratum complexum pontis, which is disposed transversely between the decussating fibers of the middle cerebellar peduncle. These laminae of gray matter continue upward irregularly and as the upper portion of the pons is approached they tend to focus ventrally and dorsally, the dorsal group joining the deep layer of the pontile nucleus, to form a support for the substantia nigra, while the ventral group tends to coalesce ventrally and forms a thickened mass of gray matter into which the cerebral peduncle enters as it passes from the mesencephalon into the metencephalon. In the region where the superior cerebellar peduncle enters the brain stem, the pontile nucleus arrives at its greatest expansion, for here the deep layer of the pontile nucleus swings dorsally to embrace the reticular formation almost as far dorsal as the junction of the dorsal and middle thirds of the brain stem. The various laminae of the pontile nucleus are arranged somewhat concentrically, all corresponding to the curve of the surface of the brain stem, and end in irregular, jagged extremities from between which stream the middle cerebellar peduncular fibers as they converge to form the middle peduncle of the cerebellum on the lateral aspect of the metencephalic portion of the brain stem. The definite condensation of the pontile nuclei to form the buttresses upon which rests the substantia nigra is not so clearly evident in this reconstruction of the human brain stem as it was in some of the lower forms, on account of the fact that the greater mass of the peduncular fibers serves to break up the lateral buttress into a number of small laminae and groups of nuclear material.

The transition from the pontile nucleus to the substantia nigra is so gradual and indistinct that it is difficult to say at which point the deep layer of pontile nucleus and the ventral layer of the reticular formation cease and the substantia nigra begins. In the cephalic portion of the metencephalon the pontile nucleus is deficient on its lateral and latero-dorsal aspects, supplying a point of entrance for the cerebral peduncle as it passes ventrolateral to the substantia nigra, the peduncle being enveloped on its dorsal, mesial and ventral surfaces but free on its lateral surface as it enters the metencephalon.

The Vestibular Nuclei

This mass of gray matter first appears at about the level of the opening of the fourth ventricle as the nucleus of the descending root, interposed between the gray matter of the floor of the fourth ventricle and the diminishing nucleus of Burdach and appearing almost as a cephalic continuation of this nucleus. It is more or less pyramidal in shape, its base being supported by the gray matter forming the floor of the fourth ventricle while its apex is directed outward ventrolaterally and is inserted between the substantia gelatinosa trigemini and the corpus restiforme.

The nucleus of Deiters definitely appears in the vestibular area at the lower portion of the fourth ventricle and continues to increase in size until it reaches the mid-ventricular level of the stem. From this point it diminishes and rapidly comes to a termination below the level at which the substantia gelatinosa trigemini disappears within the reticular formation. Prior to its disappearance the nucleus of von Bechterew appears as a dorsal extension of the vestibular area in the lateral wall of the fourth ventricle.

The nucleus of Schwalbe or the triangular nucleus of the vestibular complex appears as a triangular field lying directly subjacent to the gray matter forming the floor of the fourth ventricle and mesial to the nucleus of Deiters. It rapidly increases in size, being quite extensive transversely, and bulges forward to come into contact with the dorsal surface of the reticular formation ventrally. Its greatest size corresponds with the maximum development of the nucleus of Deiters. It then rapidly diminishes in size and entirely disappears at the level of the nucleus of von Bechterew. At its acme it occupies the lateral three-fifths of the subependymal portion of the gray matter of the floor of the fourth ventricle in the mid-ventricular portion, forming a considerable eminence on the ventricular floor, the acoustic eminence, but its cephalo-caudal extent is relatively insignificant. Its lowest extremity corresponds with the upper level of the cochlear nucleus and its upper limit with the nucleus of von Bechterew, thus occupying the middle portion of the fourth ventricle.

The Cochlear Nuclei

These nuclei make their appearance at a level slightly below the mid-point of the medullary portion of the fourth ventricle as a collection of nuclear material adjacent to the lateral angle of the fourth ventricle. This mass of gray matter is the dorsal cochlear nucleus. It gradually increases in thickness and at the same time extends laterally over the acoustic nerve root, conforming to the surface contour of the corpus restiforme which lies immediately subjacent to it.

The nuclear material gradually extends more and more laterally and ventrally and thickening at its distal extremity it becomes a discrete ventral nuclear collection called the ventral cochlear nucleus. It occupies the ventro-lateral angle of the oblongato-pontile junction, its most ventral extent lying somewhat in front of the mid-point on the lateral surface of the brain stem. The cochlear nerve root passes through the mesial aspect of the ventral cochlear nucleus, splitting it into two portions, a lateral mass which overlies the root as an oval collection of gray matter, and a mesial portion existing as a flat lamina of nuclear tissue applied to the mesial aspect of the entering root.

In the more caudal portion of the cochlear complex the ventral and dorsal nuclei are joined together by a well-defined layer of nuclear material. This layer becomes thinner and thinner as the corpus restiforme moves dorsally toward its entry into the inferior cerebellar peduncle until a definite separation between the two cochlear masses results in the formation of two discrete nuclei, the dorsal and ventral. A small portion of the dorsal cochlear nucleus persists independently in the angle of the floor and lateral wall of the lateral ventricle, while the typical oval-shaped mass of nuclear material, the ventral cochlear nucleus, continues cephalad and somewhat ventrad as a separated mass of gray matter. The nucleus continues upward to the level of the definitive appearance of the pontile nucleus where it rather abruptly terminates. The cochlear complex in the human brain stem is much more extensive than that found in the lower forms, the nuclear material being scattered richly between the fibers of the nerve as that structure approaches the brain stem, producing a continuous and definite nuclear connection between the dorsal and ventral accumulations of gray matter. At its junction with the fourth ventricle the cochlear nucleus shows its greatest dimensions, the dorsal nuclear subdivision being continued mesially under the floor of the fourth ventricle, separating the subependymal gray matter of the fourth ventricle for a considerable distance from the dorsal surface of the vestibular complex.

The Colliculi

These masses of gray matter appear to be relatively insignificant in the reconstruction of the gray matter of the human brain stem. In particular the inferior colliculus is represented by a relatively small collection of nuclear material. It rests upon the cephalic continuation of the deep layer of the reticular formation in the mesencephalon, this nuclear matrix separating the colliculus itself from the gray matter surrounding the aqueduct of Sylvius. The colliculus itself is made up of a number of layers of gray matter, the most definite of which is the external layer which is represented in the reconstruction. The interior of the colliculus is formed very largely of white fibers and as these fibers approach each other and coalesce they form a fibrous core for the colliculus. Arising from the lateral aspect of the colliculus is a bundle of fibers, the inferior brachium, which leaves the colliculus and passes toward the mesial geniculate body, producing a deep groove and in some places a tunnel in the lateral surface of the mesencephalic reticular formation. The inferior colliculus is supported laterally by the lateral extension of the reticular formation while mesially it rests upon the reticular formation forming the dorsal raphe of the mesencephalon and a group of fibers which emerge from the colliculus and cross to the opposite side as the commissure of the inferior colliculus. It is separated cephalically from the superior colliculus by a dorsal extension of the reticular formation. This dorsal prolongation arises from the deep layer of the mesencephalic reticular formation extending dorsally and then mesially to join its fellow of the opposite side at the mid-line, thus separating the superior and inferior colliculi from contact with one another.

The superior colliculus is considerably more extensive cephalo-caudad than the inferior colliculus and appears as a nuclear specialization in the reticular formation which surrounds it on all sides and separates it from the inferior colliculus caudally, its fellow of the opposite side mesially and the thalamic nuclei cephalically. Mesially the superior colliculi are separated from one another by a continuation upward of the indifferent reticular formation which separates the inferior from the superior colliculi. Mesially the superior colliculus rests upon a mass of fibers which arise from the interior of the superior colliculus, converge toward each other at the midline and cross to join the superior colliculus of the other side, thus forming the commissure of the superior colliculus. The development of this mass of fibers in this region definitely separates the superior colliculus from the gray matter surrounding the aqueduct of Sylvius. Laterally and ventrally the superior colliculus is supported by the gradually increasing bulk of the reticular formation, which appears cephalad and dorsad to the intertegmental course of the superior cerebellar peduncle. Cephalically, the superior colliculus gradually decreases in thickness and losing its characteristic appearance, it becomes a part of a thin lamina of indifferent gray matter which fuses with the habenular region of the dienecephalon.

The Substantia Nigra

The substantia nigra appears as a relatively massive collection of gray matter in the ventral portion of the mesencephalon and seems gradually to differentiate itself from the fused nuclear material forming the ventral layer of the reticular formation and the dorsal layer of the pontile nucleus. This change occurs very gradually and it is difficult to say at which point the fused reticulo-pontile gray matter ceases and the distinctive, characteristic neural tissue of the substantia nigra appears. It is supported by the pontile nucleus, the formation of the two buttresses already mentioned not being nearly so definite in man as it is in some of the lower forms. The substantia nigra rapidly increases in bulk and spreads laterally, its deep surface being separated from the tegmental reticular formation by the beginning condensation of fibers which in the diencephalon will form the fields of Forel. Laterally the substantia nigra is continued outward into two definite prolongations which are produced by the appearance of a mass of white fibers in the lateral portion of the substantia nigra, arising from a definite nuclear condensation. In the interpeduncular region the mesial extremity of the substantia nigra is separated from its fellow of the opposite side by the indifferent gray matter forming the interpeduncular space, while the reticular formation as it gradually becomes reconstituted after the decussation of the superior cerebellar peduncles moves forward and then swings laterally to parallel the dorsal surface of the substantia nigra thus completely separating the substantia nigra from the nucleus ruber.

The Nucleus Ruber

This large mass of gray matter appears in the ventromesial portion of the mesencephalic tegmentum above the cavity excavated from the reticular formation by the decussation of the superior cerebellar peduncles. It is a distinct globular nuclear mass and rapidly increases in size, presenting the spherical appearance so typical of it and becoming the most striking structure in the mesencephalic tegmentum. It is rounded in form and completely surrounded by a capsule or mantle of white fibers which separates it from the reticular formation.

The Central Gray Matter

A thin lamina of gray matter is seen extending backward from the central gray matter as a narrow tongue lining each side of the dorsomedian sulcus. This layer of gray matter continues to move dorsally and then rapidly expands as the fourth ventricle opens. It is disposed in an arched fashion laterally corresponding with the opening of the fourth ventricle and develops into a layer of gray matter which forms the floor of the fourth ventricle and is interposed between the ependymal lining of the ventricle itself and the dorsal medullary nuclei. This thin layer of gray matter continues upward, increasing considerably in lateral extent, fusing with the dorsal cochlear nucleus and forming a thin layer over the triangular nucleus of the vestibular complex. In its lower portion it is in direct contact ventrally with the hypoglossal nucleus which appears as the eminentia hypoglossi on the floor of the ventricle as that structure opens. Lateral to this eminence appears a depression which separates theem inentia hypoglossi from another elevation, the eminentia vagi, which is produced by the underlying dorsal nucleus of the vagus.

From this point upward the floor of the fourth ventricle is rather smooth and appears as a thin sheet of gray matter extending from the median sulcus of the ventricle to the lateral ventricular wall. At about the mid-portion of the ventricle another eminence appears near the midline of the floor of the fourth ventricle. This elevation is produced by the development in this locality of the abducens nucleus and is called the eminentia abducentis. These eminentiae are relatively high, the groove between them being quite deep. The area which corresponds with the vestibular and dorsal cochlear nuclei, known as the acoustic area, is relatively smooth and is continued laterally into the lateral recess of the fourth ventricle at the point of entrance of the cochlear division of the acoustic nerve. The gray matter of the floor of the fourth ventricle is continued upward, furnishing a thin covering for the triangular nucleus of Schwalbe and the nucleus of von Bechterew in the lateral wall of the fourth ventricle.

The central gray matter forming the floor of the fourth ventricle above the mid-ventricular region rapidly contracts in its lateral dimension and, thickening, it begins to assume the characteristic appearance of the gray matter surrounding the aqueduct of Sylvius. As the mesencephalon is approached the cavity of the ventricle rapidly diminishes, the walls of the ventricular system increase considerably in thickness until the region of the colliculi is approached, where the lumen of the ventricle rapidly diminishes in size and the walls of the ventricle become enormously thickened. This thickening takes place ventral and dorsal to the aqueduct throughout the lower half of the mesencephalon, the dorsal portion forming the support for the mesial extremities of the superior and inferior colliculi. This dorsal layer of gray matter is pierced at various points by the fiber bundles which are passing across between the two inferior and the two superior colliculi as the collicular commissures. In the upper half of the mesencephalon the ventral portion of the central gray matter rapidly extends ventrally, forming a long, tongue-shaped process which passes forward lateral to the raphe and almost in contact with its fellow of the opposite side, being separated only by the indifferent material of the raphe. In this ventral extension of the central gray matter there appears a large nucleus, the nucleus of the oculomotor nerve, which is continued cephalad to the junction of the mesencephalon with the diencephalon.

In the uppermost portion of the reconstruction the dorsal portion of the central gray matter is broken up by the appearance of the posterior commissure which passes across from one side to another and divides this part of the central gray matter into a ventral lamina lying directly around the cavity of the aqueduct of Sylvius and a dorsal layer which lies between the posterior commissure and the commissure of the superior colliculi. Laterally the central gray matter is supported almost throughout its entire extent by the reticular formation of the various portions of the stem. In the upper portion of the mesencephalon the forward prolongation of the central gray matter, which contains in its subaqueductal region the oculomotor nucleus, is continued ventrally into the interpeduncular space and there becomes continuous with the interpeduncular formation which is being transformed into the zona incerta. This interpeduncular gray matter is continued forward and merges with the gray matter forming the hypencephalon.

Chapter XXVII

THE BRAIN OF PREHISTORIC MAN

A Survey of the Psychological Foundations of Human Progress

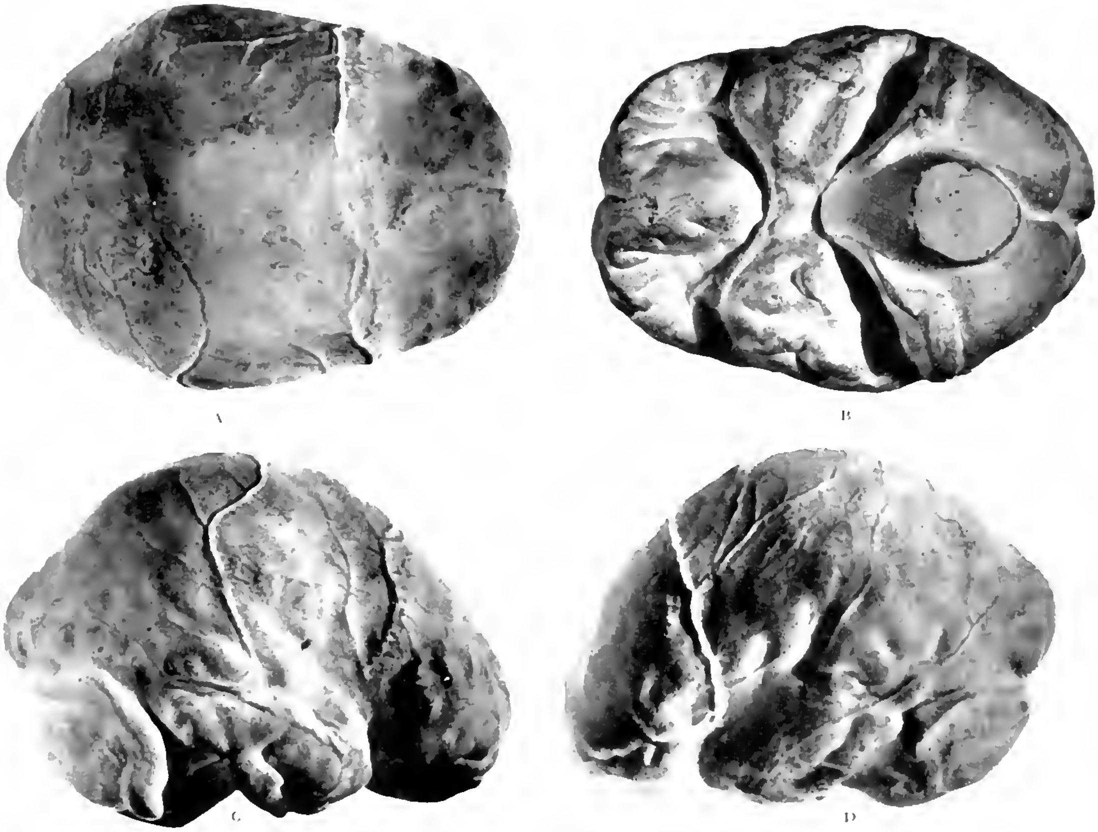
THE human family, according to most conservative authority, has been in existence more than a half million years. During all the vast era of Pleistocene time, with its recurrent glaciations and intervals of warmth, man's brain steadily grew. This growth at first was slow and irregular. Later it became so decisive as to make cerebral development one of the most striking features in human evolution. The brain slowly increased in volume. It acquired much refinement in many structural details. Its newer parts became more highly specialized. As a result of the evolutional process the brain of modern man is a far more efficient organ than that possessed by the earliest of human kind.

It is probable that many distinct species of prehistoric man inhabited the earth. Several distinct races have already been identified by means of fossilized human bones. The racial differentiations established in this manner have been utilized to reconstruct the outward appearance of these prehistoric peoples. In the reconstructions of Professor McGregor, the differences are striking (p. 732). The ape-like appearance of Pithecanthropus erectus affords some reasons for calling this earliest known member of our family circle the Ape-man. The old man of Cro-Magnon, on the other hand, possesses a nobility of expression which in itself seems to justify his characterization as the "Paleolithic Greek." Between these two extremes, the Neanderthal and Piltdown men are intermediate stages. How these ancient people felt, thought and lived is a matter of importance, concerning which the brain has much to reveal. This revelation is most significant, because of its disclosures regarding the cultural progress and possibilities of mankind.

Fossil Evidence in the Study of the Brain of Prehistoric Man

In order to gain some idea of what the brain of primitive man was like, it is necessary to depend upon certain circumstantial evidence. This admission may seem to put the case in its most unfavorable light. The fact remains that the brain of man shared the same fate as other soft parts of his body; but it has not disappeared without leaving definite impressions of its size and shape. These impressions have been found upon fossilized cranial bones dating back to the earliest human races yet recognized. There is, of course, some question as to the value of such impressions in drawing conclusions about the brain. Professor Symington, who has investigated the subject extensively by means of endocranial casts, is extremely cautious in the matter. He prefers to admit frankly the limitations of our knowledge rather than reconstruct the brain of primitive man upon too slender evidence. This wise admonition has been borne in mind throughout the following descriptions of the prehistoric human brain.

For the purpose of sensing the full value of endocranial evidence, it is important to recall that the bony capsule enclosing the brain is peculiarly susceptible to the effects of cerebral growth. Some portions of this capsule begin to form in cartilage and some in membrane. Four cranial bones have a membranous origin, i.e., the frontal, the parietal, the occipital, and the squamous portion of the temporal bone. Expansion of the brain appears to be the dominant factor in the growth of the head. In consequence, the membranous bones of the skull bear many impressions of the cerebral hemispheres. These impressions would be more pronounced if the cerebral convolutions came into actual contact with the inner surface of the skull. But the interposition of the dura mater, the pia mater, the arachnoid and the cerebrospinal fluid in part obscures the imprint of the brain. A number of cerebral features, however, are consistently impressed upon the endocranium. Schwalbe has shown that there are certain bony ridges corresponding to cerebral fissures and a number of depressions produced by cerebral convolutions. These he called respectively *juga cerebralia* and *impressiones digitatae*.



FIGS. 362 TO 365. FOUR VIEWS OF AN ENDOCRANIAL CAST OF A MODERN HUMAN SKULL SHOWING THE IMPRESSIONES DIGITATAE AND JUGA CEREBRALIA OF SCHWALBE WHICH INDICATE THE POSITION OF SEVERAL CONVOLUTIONS, FISSURES AND ARTERIES OF THE BRAIN.

A Vertex or Dorsal Surface of the Brain. B Base or Ventral Surface. (C) Right Lateral Surface. D Left Lateral Surface. Illustrating those markings which may be looked for in an endocranial cast.

Juga and impressions appear in the separate cranial bones as follows (Figs. 362–365):

Table A

PRINCIPAL FOSSIL REMAINS OF PREHISTORIC MAN

(Pre-Paleolithic and Lower Paleolithic)

Antiquity (years)	Name	Race	Discoverer	Place and date	Parts	Period
500,000	Pithecanthropus erectus	Trinil	Dubois	Java 1891	Skull cap Teeth (3) Femur	Eolithic ?
250,000	Paleoanthropus heidelbergensis	Heidelberg	Schoetensack	Heidelberg 1907	Lower jaw with teeth	Eolithic ?
150,000	Eoanthropus dawsoni	Piltdown	Dawson	Sussex 1911	Parts of skull and jaw	Early Paleolithic
130,000	Homo rhodesiensis	Rhodesian	Harris	Rhodesia 1921	Fragments of femur, tibia, sacrum. Skull (no lower jaw)	?
120,000	Homo neanderthalensis	Neanderthal	Flint	Gibraltar 1848	Skull	Early Paleolithic (probably)
120,000	Homo neanderthalensis	Neanderthal	Bourret and Regnault	Malarnaud 1888	Jaw (m)	Early Paleolithic (probably)
120,000	Homo neanderthalensis	Neanderthal	?	Arcy sur Cure 1859	Jaw (m)	Early Paleolithic (probably)
120,000	Homo neanderthalensis	Neanderthal	?	Gourdan ?	Fragment of lower jaw	Early Paleolithic (probably)
120,000	Homo neanderthalensis	Neanderthal	Dupont	La Naulette 1866	Lower jaw	Early Paleolithic (probably)
120,000	Homo neanderthalensis	Neanderthal	Torrent	Bañolas 1887	Lower jaw	Early Paleolithic (probably)
120,000	Homo neanderthalensis	Neanderthal	Fuhlrott	Neanderthal 1856	Top of skull, a number of skeletal fragments	Early Paleolithic (probably)
120,000	Homo neanderthalensis	Neanderthal	Rzehak	Ochos 1906	Fragment of lower jaw	Early Paleolithic (probably)
75,000	Homo neanderthalensis	Neanderthal	Nehring	Ehringsdorf and Taubach 1892-1914	Lower jaw, 2 teeth, decidual. Fragments of child's skeleton, 3 fragments of skull-cap, femur	Pre-Mousterian or Acheulean ?

TABLE A—Continued

PRINCIPAL FOSSIL REMAINS OF PREHISTORIC MAN

Pre-Paleolithic and Lower Paleolithic

Antiquity (years)	Name	Race	Discoverer	Place and date	Parts	Period
75,000	Homo neanderthalensis	Neanderthal	Kramberger	Krapina 1899	Fragments of skulls, skeletons of 11 (?) individuals	Pre-Mousterian or Acheulean ?
75,000	Homo neanderthalensis	Neanderthal		Neu-Essing Klause	1 molar	Pre-Mousterian or Acheulean ?
75,000	Homo neanderthalensis	Neanderthal		Galilee 1926	Skull	?
75,000	Homo neanderthalensis	Neanderthal		Gibraltar II 1926		?
50,000	Homo neanderthalensis	Neanderthal	Hauser	Le Moustier 1908	Skull, crushed. Skeleton. Ceremonial burial	Mousterian
50,000	Homo neanderthalensis	Neanderthal	Kample	Ehringsdorf 1914	Jaw. See Taubach	Mousterian
40,000	Homo neanderthalensis	Neanderthal	Maska	Šipka 1882	Fragment of lower jaw	Mousterian
40,000	Homo neanderthalensis	Neanderthal	Bouyssonie Bardon	La Chapelle aux Saints 1908	Skull (in almost complete). Skeleton. Ceremonial burial	Mousterian
40,000	Homo neanderthalensis	Neanderthal	Martin	La Quina 1911	Skull + well-preserved skeleton. Child's skull, skeletal fragments	Mousterian
30,000	Homo neanderthalensis	Neanderthal	Peyrony and Capiton	La Ferrassie 1909-1910	Skeletons (incl. 2 adults, 4 children. Ceremonial burial	Mousterian
30,000	Homo neanderthalensis	Neanderthal	Peyrony	Pech de L'Azé 1909	Skull of child	Mousterian
30,000	Homo neanderthalensis	Neanderthal	Peyrony	Petit-Puymoyen 1907	Fragments of jaws (maxillae	Mousterian
30,000	Homo neanderthalensis	Neanderthal	Puydt Fraipont and Lohest	Spy 1887	2 skeletons	Mousterian
30,000	Homo neanderthalensis	Neanderthal	Marett	Jersey 1910	13 teeth	Mousterian

Table B

PRINCIPAL FOSSIL REMAINS OF PREHISTORIC MAN

(Upper Paleolithic)

Antiquity (years)	Name	Race	Discoverer	Place and date	Parts	Period
25,000	Homo sapiens	Cro-Magnon	?	Aurignac 1852 ?		Aurignacian
25,000	Homo sapiens	Cro-Magnon	Lartet	Cro-Magnon 1868	4 individuals: 1 fetus, 2 men and 1 woman, well-preserved	Aurignacian
25,000	Homo sapiens	Cro-Magnon	Verneau	Grotte des Enfants 1884 (Grimaldi)	6 skeletons (2 negroid)	Aurignacian
25,000	Homo sapiens	Cro-Magnon	Rivière	Grotte du Cavillon 1872 (Grimaldi)	1 skeleton (6.55 m). Packet of bones in ochre at the base	Aurignacian
25,000	Homo sapiens	Cro-Magnon	Abbo	Barma Grande ? (Grimaldi)	6 skeletons	Aurignacian
25,000	Homo sapiens	Cro-Magnon	?	Baousso da Torre	2 skeletons (adult). Bones of child	Aurignacian
25,000	Homo sapiens	?	Hauser	Combe Capelle 1907	1 skeleton	Aurignacian
25,000	Homo sapiens	?	Sierra	Camargo ?	Skull fragments	Aurignacian
25,000	Homo sapiens	?	Obermaier	Willendorf 1908	Fragments of femur, humerus, upper and lower jaws	Aurignacian
25,000	Homo sapiens	Cro-Magnon		Enzheim	1 skeleton	Aurignacian
25,000	Homo sapiens	Cro-Magnon		Paviland 1823	1 skeleton	Aurignacian
25,000	Homo sapiens	Cro-Magnon		Ojcow	1 skull-top	Aurignacian
25,000	Homo sapiens	(Sub-brachyceph. Not Cro-Magnon)	Depéret Arcelin and Mayet	Solutré	5 skeletons	Aurignacian
20,000	Homo sapiens	?	Daleau	Pair-non-Pair 1896	Skull fragments (parietal)	Solutrean
20,000	Homo sapiens	?	Vire	Lacave ?	Frontal skull fragments	Solutrean
20,000	Homo sapiens	?	?	Roset ?	Teeth	Solutrean
20,000	Homo sapiens	Predmost or Brünn ?	Maška Kriz Wankel	Predmost 1880	14 skeletons. Remains of 6 (?) other individuals	Solutrean
20,000	Homo sapiens	Brünn ?	Makowsky	Brünn 1891	1 skeleton	Solutrean
20,000	Homo sapiens	Brünn ?	Hillebrand	Ballahohle	1 child's skull	Solutrean

TABLE B—*Continued*

PRINCIPAL FOSSIL REMAINS OF PREHISTORIC MAN

Upper Paleolithic

Antiquity years	Name	Race	Discoverer	Place and date	Parts	Period
20,000	Homo sapiens			Laugerie-Haute	1 skeleton	Solutrean
20,000	Homo sapiens			Neu-Essing	1 skeleton	Solutrean
15,000	Homo sapiens	Cro-Magnon	Cartailhac	La Madeleine 1864	1 skeleton	Magdalenian
15,000	Homo sapiens	Cro-Magnon	Massenat	Laugerie-Basse 1872	1 skeleton	Magdalenian
15,000	Homo sapiens	?	Testut	Chancelade 1888	1 skeleton	Magdalenian
15,000	Homo sapiens	Cro-Magnon		Cap-Blanc	1 skeleton	Magdalenian
15,000	Homo sapiens	Cro-Magnon		Duruthy	1 skeleton	Magdalenian
15,000	Homo sapiens	Cro-Magnon	Tournier	Les Hoteaux	1 skeleton	Magdalenian
15,000	Homo sapiens	Cro-Magnon	Karsten	Freudenthal 1874	Skeletal and skull fragments (parietal, mandible, teeth)	Magdalenian
15,000	Homo sapiens	Cro-Magnon		Le Placard 1883	1 skull (f), 9 cups made of skull-tops. Skeletal fragments	Magdalenian
15,000	Homo sapiens	Cro-Magnon	Verworn Bonnet Steinmann	Obercassel 1914	2 skeletons	Magdalenian
15,000	Homo sapiens	Cro-Magnon	Bouyssonie	Limeuil	Skull fragments	Magdalenian
15,000	Homo sapiens	Cro-Magnon		Grotte des Hommes	3 skulls	Magdalenian
15,000	Homo sapiens	Cro-Magnon	Daleau	Grotte des Fees	Fragments of upper and lower jaws	Magdalenian
15,000	Homo sapiens	Cro-Magnon	Breuil	Lussac	Lower jaw	Magdalenian
15,000	Homo sapiens	Cro-Magnon	Piette	Mas d'Azil	1 skull top	Magdalenian
15,000	Homo sapiens	Cro-Magnon	Nelli	Espelugues of Lourdes	Various fragments	Magdalenian
15,000	Homo sapiens	Cro-Magnon		Castillo	2 skull fragments worked into bowls or cups (child's lower jaw, 1 adult molar. Aurig.	Magdalenian
15,000	Homo sapiens	?		Furfooz	Skull	Uncertain. Probably Neolithic
10,000	Homo sapiens	?	R. R. Schmidt	Ofnet	33 skulls	Azilian
10,000	Homo sapiens	Cro-Magnon		Hexenküche Bavaria	1 skull	Azilian

In the Frontal Bone:

Pars squamosa, the superior frontal convolutions

Pars orbitalis, the orbital convolutions

Pars temporalis, the inferior frontal convolution.

In the Parietal Bone:

Postero-inferior triangle (Schwalbe), usually some impressions of the parietal convolutions

The parietal fossa corresponding to the parietal eminence

The crista Sylvii, marking the horizontal ramus of the Sylvian fissure.

In the Temporal Bone:

Pars squamosa with the greater wing of sphenoid, the middle temporal sulcus and the second and third temporal gyres.

In the Occipital Bone:

The impressiones occipitalis, crista occipitalis, crista marginalis and the juga cerebellaria.

In the fossilized skull these features become landmarks of utmost importance as guides in establishing functional localization in the brain of primitive man.

The more important fossilized skulls, discovered either in part or largely intact, are given in the accompanying tabulations. To the data are added the names of the discoverers, the place and date of the discovery. Further specifications are included to indicate, is so far as possible, the estimated antiquity and the race of man to which each fossil specimen has been accredited (Tables A and B).

The Brain of Pithecanthropus Erectus, the Ape-Man of Java

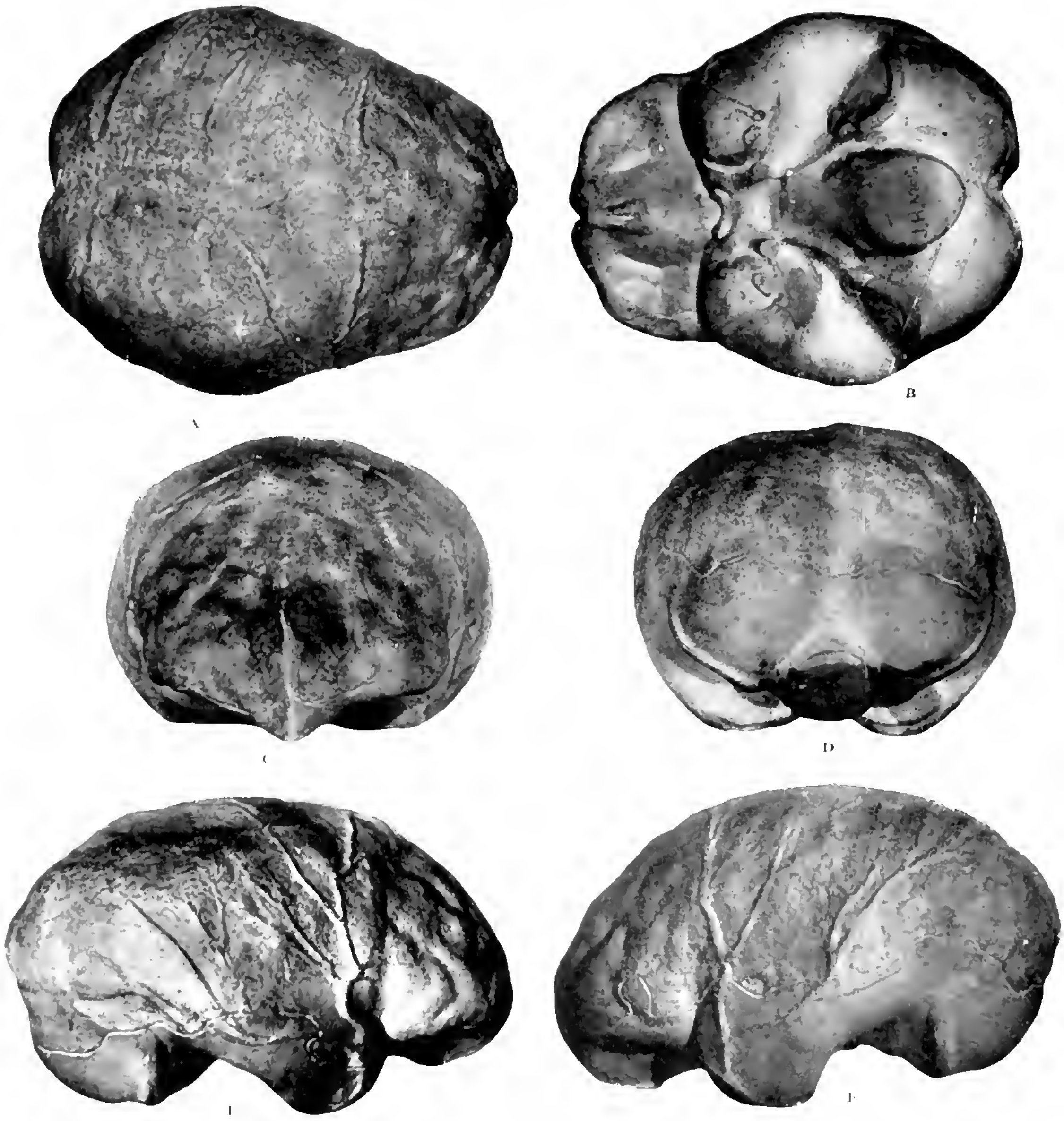
According to prevailing opinion, the most ancient human fossil is that of Pithecanthropus erectus. To it an antiquity of not less than 500,000 years is assigned. Although the humanity of this fossil is disputed by some authorities, the testimony it bears indicates a primate standing relatively high in the scale. The fossilized part of the skull consists of the calvarium which includes the greater portion of the frontal squamosa and the parietal bones, a part of the occipital bone and perhaps a small fragment of one temporal squamosa. The preservation is fairly symmetrical on the two sides of the cranium. For further descriptions of this fossil, the reader is referred to Dubois' monographs on the subject.

IMPRESSIONS AND JUGA OF THE CALVARIUM

The calvarium is particularly fortunate because it retains many significant impressions and juga indicating the configuration of the brain. A cast made from the pithecanthropus calvarium reveals a number of features which furnish valuable information concerning the brain of the Javan man. The parietal area shows clearly the distribution of the middle meningeal artery, also the eminence and groove corresponding respectively to the parietal fossa and crista Sylvii. Reproductions of the brain cast of pithecanthropus, together with supplementary reconstruction of the cerebral base by Professor McGregor are shown in Figures 366 to 371. The relief in the occipital region marks the grooves and convolutions corresponding to the occipital impressions, the crista occipitalis, the crista marginalis and the juga cerebellaria.

From these data it is possible to introduce certain boundaries upon the lateral surface of the cast and thus establish the probable position of several functional areas in the brain.

The Sylvian Fissure. The horizontal branch of the Sylvian fissure extends from the frontotemporal notch to the lower margin of the parietal eminence. The full extent and terminal disposition of this fissure cannot be determined and hence it is not possible to indicate the character or position of the supramarginal convolution.



FIGS. 366 TO 371. SIX VIEWS OF THE ENDOCRANIAL CAST OF PITHECANTHROPUS ERECTUS (JAVAN APE-MAN) THE MOST PRIMITIVE KNOWN REPRESENTATIVE OF THE HUMAN FAMILY. ESTIMATED ANTIQUITY OF FOSSIL 500,000 YEARS. RESTORATIONS BY PROF. J. H. MCGREGOR.

A Vertex. B Base Restored. C Frontal Pole. (D) Occipital Pole. (E) Right Lateral Surface. F Left Lateral Surface. The frontal convolutions and branches of the middle meningeal artery are especially well defined. The smoother areas in the cast indicate the regions which have been restored.

THE FISSURE OF ROLANDO. The fissure of Rolando (sulcus centralis) may in a general way be placed between the two main branches of the middle meningeal artery and in front of the parietal eminence. Estimated by the anthropometric criteria of this fissure now generally accepted, the upper extremity of the fissure may be placed on or near the superior longitudinal groove about 2 cm. posterior to its midpoint, calculated as one half the distance from the frontal to the occipital end of this groove. The general direction of the Rolandic fissure may likewise be estimated as a descending line which leaves the superior longitudinal groove at an angle of inclination forward of somewhere between 67° and 71.4°. The allocation of this most important boundary is extremely generalized and must of necessity omit many essential details of the sulcus. It affords no intimation as to the extent of the fissure, or the relations of its upper and lower extremities to the superior longitudinal fissure on the one hand and the fissure of Sylvius on the other. Neither does it denote the presence of the usual genuflections conspicuous in the human central sulcus. The position and disposition of the Rolandic fissure assigned to the brain of pithecanthropus depend more upon deduction and analogy than actual indications on the cast. It is desirable, however, to establish certain approximations regarding the character and position of this fissure.

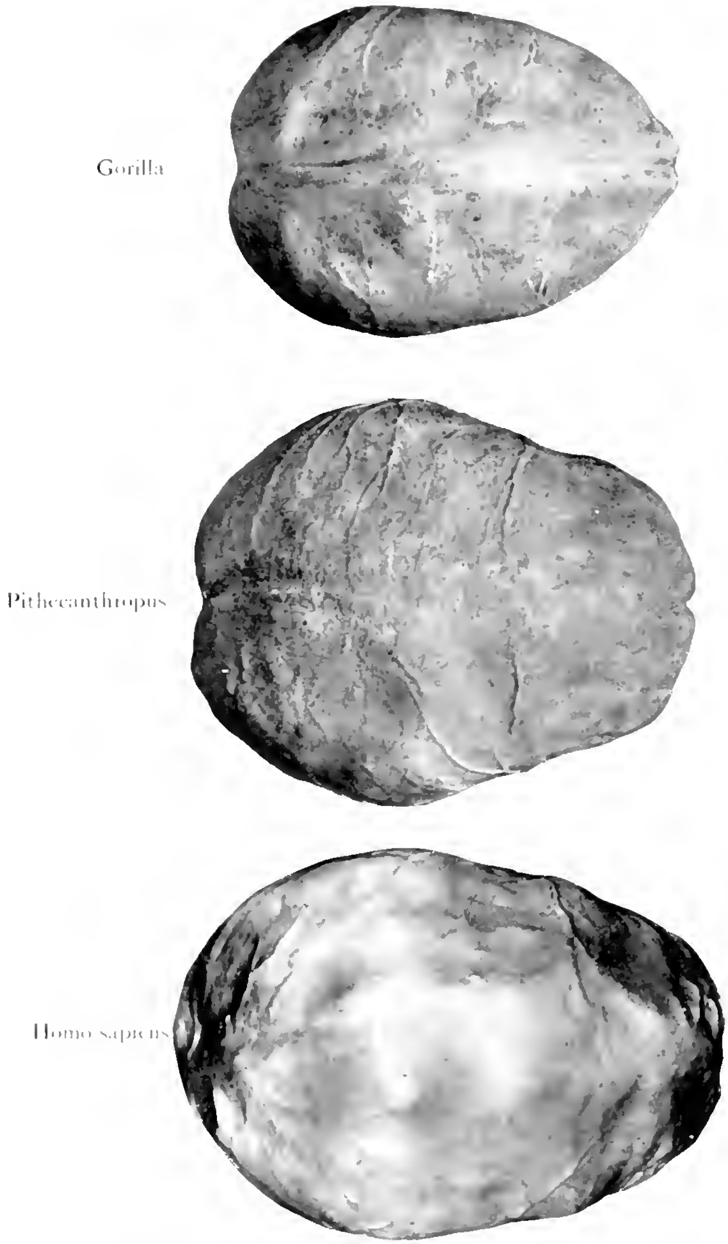
THE GROOVE OF THE TRANSVERSE SINUS. The third landmark is the groove of the transverse sinus which indicates the planes of separation between the occipital lobes of the cerebral hemispheres and the cerebellum. This groove with the superior longitudinal furrow marks the position of the torcula herophili.

These boundary lines determine the general extent of four great lobes in the brain, namely, the frontal, parietal, temporal and occipital. It is possible in the light of this topography to consider the characters and significance of each lobe separately.

THE FRONTAL LOBE OF PITHECANTHROPUS ERECTUS

The frontal lobe appears as a particularly conspicuous portion of the hemisphere (Fig. 366). It is prominent especially because of its large size and pronounced convolutions. Near the middle of the frontal convexity and in juxtaposition with the superior longitudinal fissure is a prominent Pacchionian enlargement. The relief of the frontal convolutions is especially noteworthy as it gives this region of the brain an individuality possessed by no other area. This observation does not imply that the convolutional process is supreme in the frontal lobe of pithecanthropus. It demonstrates, as Schwalbe has previously shown, that the frontal squamosa is more impressionable to brain growth than other parts of the skull. It is fortunate, moreover, that such is the case, for it is this region of the hemisphere which has most to reveal regarding the higher psychic development of the brain. Nor should it be overlooked that this frontal lobe represents the latest accessions of human specialization, whereby man has distinguished himself in creation and finally acquired all that is implied in the title, "Homo sapiens."

There is a slight asymmetry in the size and shape of the frontal lobes, the left being somewhat larger. This also applies to the frontal convolutions of the left side. In relative size the frontal area represents upon its lateral surface more than one-third of the entire exposed convexity of the hemisphere. The two frontal lobes together, when viewed from above, give the impression of a truncated pyramid. There is a marked bluntness at the frontal pole and the outlines extend backward with a gradual widening to the level of the Rolandic fissure. This general broadening is not consistently maintained. In one zone there appears to be a considerable constriction. For purposes of subsequent identification this zone is called the *coronal constriction*. It begins at either frontotemporal notch and follows the impression of the coronal suture to the midline.



FIGS. 372 TO 374. A COMPARISON OF THE ENDOCRANIAL CASTS OF GORILLA, PITHECANTHROPUS AND HOMO SAPIENS. THE PRINCIPAL EVOLUTIONARY EXPANSION APPEARS IN THE FRONTAL LOBE.

Frontal Lobe of Pithecanthropus as Compared with That of Gorilla and Homo Sapiens. As compared with the primate frontal lobe nearest to that of man, i.e., the gorilla, the brain of pithecanthropus shows manifest differences (Fig. 372). The frontal lobe as a whole is much less conspicuous in gorilla. It is actually and relatively smaller in size. The relief of its convolutions is much less pronounced, its shape is more pyriform as it tapers towards its apex at the frontal pole and it has no coronal constriction. The left lobe of the Javan man is slightly larger than the right, which is probably indicative of unidexterity. All of these differences point to a distinctly inferior development in the frontal lobe of gorilla as compared with pithecanthropus. A comparison with the brain of Homo sapiens shows at once what decisive gains the brain of modern races has made over its simple prototype of primitive man (Fig. 374). In size and general appearance the brain of pithecanthropus resembles that of a three-year-old child.

Fissures in the Frontal Lobe. The fissures in the frontal lobe which may be identified with certainty are the superior and middle frontal sulci. They are tortuous and bound correspondingly complex convolutions. These fissures are most pronounced in the prefrontal area and cannot be traced back as far as the frontal region. The convolutions determined by the frontal sulci are the superior, middle and inferior frontal gyres. The last of these is of greatest importance since the inferior frontal convolution, especially on the left side, is almost universally regarded as the motor speech center in man. In connection with this convolution some authorities have identified the anterior and ascending branches of the Sylvian fissure. If present in pithecanthropus, however, they exist merely as the faintest traces which afford insufficient ground for their acceptance as definite cerebral landmarks. In Homo sapiens, these sulci are conspicuous and impart much prominence to the inferior frontal convolution. There is no indication of the precentral fissure and hence no actual guide to the limits of the precentral or motor convolution. How extensively this region of the cortex in pithecanthropus is provided with an intermediate precentral area for skilled movements cannot be determined. The basal surface of the frontal lobe as shown in supplementary reconstruction by Professor McGregor indicates the presence of two orbital concavities of considerable depth and well-developed interorbital keels; in other words, conditions far more primitive and pithecoid than those in modern man.

Physiological Deductions to Be Drawn from Frontal Lobe. Estimated from the physiological standpoint, the frontal lobe of pithecanthropus is indicative of a behavioral advance far above the plane of gorilla but equally below that of Homo sapiens. The Javan man must have possessed increased powers of adaptive reasoning. He was capable of more advantageous adjustment than gorilla or other anthropoids. He constructed for himself a greater sphere of experience, created at least an approach to human personality and developed the distinctive characters of individuality. It is probable also that in his manual dexterity he was right-handed; at least the greater size of his left frontal lobe suggests that his brain had singled out one hand as the chief representative for externalizing its activities. This in itself is a distinctly human character. Around it are built many of man's most productive specializations. In all of these respects the Javan man was much below his human successors. There is little in his brain by which to judge the proficiency of his manual development, to estimate how much skill he had acquired with his hands. But the prominence of his inferior frontal convolution (Fig. 375) strongly suggests that he added one supreme advantage to the motor equipment of animal life. *He had learned to speak*—to communicate in verbal language. The gradual development of skilled acts had eventually combined the effector organs of articulation and phonation into a coordinated apparatus controlled through the brain, by which he was able to express his ideas and feelings. The means of communication thus established laid the foundations of human knowledge.

The degree to which pithecanthropus may have developed language cannot be implied from anything in the external appearance of his brain. Doubtless his linguistic attainments were extremely crude. On the other hand, the fact that the cerebrum manifests such pronounced advances over the anthropoid brain in an area so intimately identified with speech in Homo sapiens signifies the decisive step which pithecanthropus had made in the development of human kind.

With all due allowance for the reservations imposed by morphological limitations, the frontal lobe of the Javan man clearly indicates that the brain had progressed in its psychic capacity, that it had expanded in those portions upon which unidexterity, reason, language and human personality depend.

THE PARIETAL LOBE OF PITHECANTHROPUS ERECTUS

The parietal lobe of pithecanthropus also gives evidence of expansion, although the details of this development are less conspicuous than in the frontal area. It is impossible to discern the relief of any convolutions, and, with the exception of the Sylvian fissure, no critical impressions may be detected. No discrete boundaries between the frontal and parietal or between the occipital and parietal lobes may be distinguished. The hypothetical position of the Rolandic fissure provides the anterior limits of the parietal area. The increased prominence of the parietal eminence, together with the general widening of the cerebrum in this region, denotes a considerable extension of the neopallium. As compared with the corresponding area in gorilla, this expansion is emphatic. In contrast to the parietal lobe of Homo sapiens, it is distinctly inferior. The parietal lobe as a whole represents the neopallial area for the elaboration of somesthetic sensibility. The expansion of this area must be regarded as incidental not only to the augmented influx of sensory impressions, but also to the increased complexity of their association.

Three somatic factors have been held especially responsible for this increase: first, the development of the human or humanoid foot; second, the assumption of the erect posture, and third, the emancipation of the hand from locomotor functions. Of these factors, the third has perhaps the greatest cogency. The increase in the parietal eminence involves a cortical area assigned to sensory perceptions of the upper extremity.

THE OCCIPITAL LOBE OF PITHECANTHROPUS ERECTUS

The occipital lobe is little more productive of cerebral landmarks than the parietal. The occipital pole of the brain extends over the cerebellum, while the divergence of the two hemispheres is pronounced in this region. A bilaterally symmetrical groove corresponding to the transverse sinus separates the cerebellum from the cerebrum and thus establishes the caudal boundary of the occipital lobe. No other boundary of this lobe is discernible in the cast nor does any indication appear either of a sulcus simiarum (sulcus lunatus — Smith) or parieto-occipital incisure. The demarcation between occipital and parietal lobes is, therefore, wholly conjectural. This latter indefiniteness, however, does not impose an embarrassment more serious than is the case with Homo sapiens, in whom the parieto-occipital dividing line is an arbitrary one. It is probable that in the human brain there is an intermediate, transitional area between the parietal and occipital lobes where the cortical types of these two regions manifest a histological mutuality. This area permits of a physiological blending in the activities of the two zones. In the apes and more particularly in the great man-like apes, a sharply defined boundary created by the sulcus simiarum exists between these two regions. No actually homologous fissure appears in the cerebrum of modern man, although several authorities maintain that the sulcus lunatus closely resembles the simian fissure and may be identified in some human brains.

In the occipital lobe on the right side a long crescent fissure begins at the superior longitudinal fissures. It curves downward and forward in the general direction of the sigmoid sinus, thus appearing both on the occipital pole and lateral convexity. Above and below it, is the relief of an occipital convolution. The markings on the left occipital lobe are less definite. A transverse ridge extends transversely outward from the lambda across either occipital area. This ridge indicates the position of the lambdoid suture.

In comparison with gorilla the occipital lobe of pithecanthropus shows considerable expansion in all diameters. As compared with the similar region in modern man this lobe appears much smaller. It seems permissible, however, to presume that in his visual organization the Javan man had advanced a long distance above any of the anthropoids. His visual associations must have been much more extensive if it is true, as seems to be the case, that he had real powers of speech. His visuo-psychic functions must have undergone notable expansion as he began to attach verbal names to what he saw about him, thus laying the foundations of that wide sphere of denomination and enumeration which mankind has created. The telencephalization of vision had made great strides in pithecanthropus. He was capable of a more effective appreciation of his environment and not the least important element in this increased effectiveness found its expression in the better control he gained over his hands through visual supervision. The many and profound influences arising from such improved visual guidance made themselves felt in innumerable ways upon his psychic organization, upon the makeup of his personality and experience, upon his capacity to learn. So also was his entire psychic life affected by the increased facility with which sensory impressions of sight, of hearing and of body sense entered into more complex associations.

THE TEMPORAL LOBE OF PITHECANTHROPUS ERECTUS

The temporal lobe in the ape-man brain is little, if at all, represented in the calvarium. Some slight portion of the superior temporal convolution may be detected, but scarcely enough to permit of more than a conjecture as to its character. The base of this lobe, as seen in the occipito-parietal region, indicates an increase in all diameters. Professor McGregor's supplementary reconstruction likewise shows decisive expansion in this lobe. The most pronounced cortical increment appears to have involved the superior and middle temporal gyres in the area assigned to auditory function. Although it seems unwise to be categorical in this matter, all of the available evidence warrants the assumption that the sense of hearing had followed the example of sight and body sense in seeking broader fields for its activities in the neopallium. Such auditory expansion is indispensable to vocal speech, since symbolic sounds are usually acquired through hearing before they may be reproduced by articulation.

All four of the great neopallial lobes of the pithecanthropus hemispheres give evidence of increased size and hence augmented functional capacity when compared with the great man-like apes. They are all, on the other hand, inferior to the similar brain regions of living races.

THE PROBABLE DYNAMIC FACTORS INDUCING BRAIN DEVELOPMENT IN PITHECANTHROPUS ERECTUS

Any opinion in the endeavor to estimate what dynamic factors induced the advanced brain development in pithecanthropus must needs be based upon conjecture. The major somatic variants in primate organization express themselves in the mode and posture of locomotion, in the differentiation of the foot and the specialization of the hand. To the reactions and interactions of these variants the primate brain has made definite responses. The cerebral area most sensitive to and most consistently affected by such modifications has been the parietal lobe. This region represents those activities engaged in sensing the body both in its axial and appendicular parts. In primates the axial segments have a greater structural fixity than the limbs whose functional adaptations have manifested a far wider range of adjustment. In this light the expansion of the sensory regions in the parietal lobe particularly related to the leg and foot, arm and hand becomes highly significant. It seems most probable that sensory increment in these areas must be an

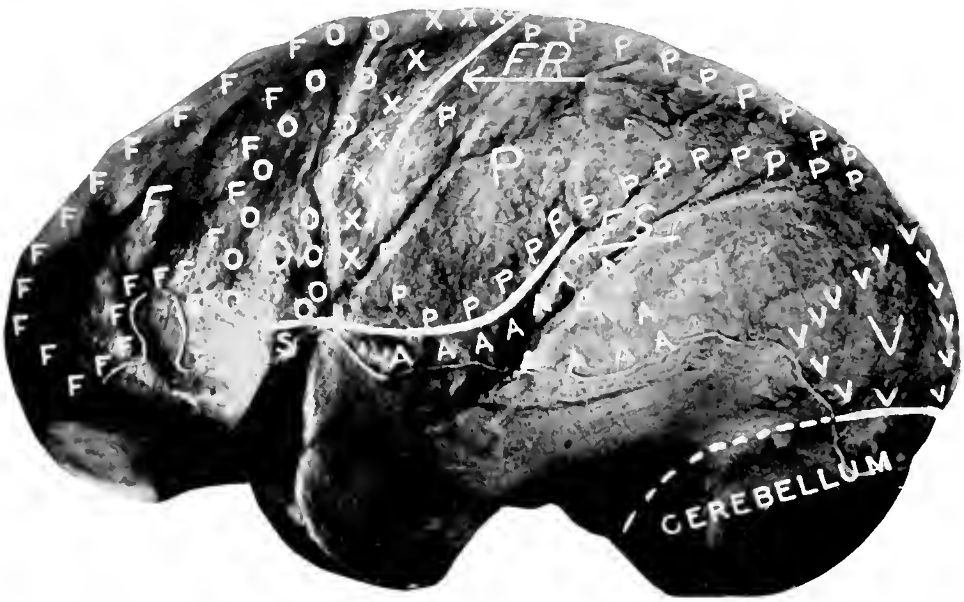


FIG. 375. FUNCTIONAL LOCALIZATION OF THE BRAIN OUTLINED UPON THE LEFT HEMISPHERE OF THE ENDOCRANIAL CAST OF PITHECANTHROPUS ERECTUS. RESTORATION BY PROF. J. H. MCGREGOR.
A, Auditory Area; F, Higher Faculties Including Personality and Reason; FR, Fissure of Rolando; FS, Fissure of Sylvius; O, Area of Skilled Movements; P, Sensory Area (Touch and Muscle Joint Sense); S, Speech Area; V, Visual Area; X, Area of Voluntary Motor Control.

essential antecedent to any expansion in the realm of more highly complex motor performance. Kinesthetic sensibility is a fundamental requisite to all skilled acts. Without it neither the motion formula nor the motor execution would be possible. For this reason the development of new sensory fields must have been closely associated with the appearance of new motor territories, if they did not actually precede them.

From the femur of pithecanthropus it is assumed that he stood and walked erect much as do his modern successors. The assumption of such erect posture entailed an extensive sequence of adaptive modifications, all of which were reflected in the brain. Standing upright in itself requires a complex sensory mechanism to receive and adjust the impulses from the proprioceptors. How intricate and essential this mechanism is may be seen in those diseases characterized by pathological changes in the sensory system. Locomotor ataxia is an outstanding example. Here the disease is confined to the sensory elements but expresses itself preeminently in the motor adjustments of standing and walking.

To what extent sensory orientation of the body is essential to proper voluntary movement is seen in such pathological conditions as acragnosis, in which the patient loses his limb sense to the degree that he may not appreciate the positions of his extremities or recognize passive movements of them. The adequate sensing of the different parts of the body in rest and action is essential to kinesthetic sensibility and the indispensable physiological basis of all voluntary movements. The transactions of this highly specialized sense are the function of the parietal lobe. As they become more extensive and complex, the parietal area has expanded to meet the new demands made upon it. Throughout the long history of primate adaptation and progress, the parietal lobe has manifested the most consistent expansion. It has especially seemed to keep pace with the progressive tendency to assume the erect posture, to develop plantigrade locomotion, to acquire bimanual characters. If the parietal expansion is a reliable index to the evolution of kinesthetic sensibility, then this essential attribute of voluntary movement became more extensive in direct proportion as the upper extremity was emancipated to perform the duties of the human hand. A simple example may suffice to elucidate this point. The individual digits in the paw of a cat or dog have not acquired independent movements similar to fingers. Their sensory representation in the brain is consequently much less, and requires less cortical area. The many individual movements of the fingers have need of much more cortical surface for their sensory orientation. It would seem to follow that the sensory demands of a foot so specialized as to support the body on the ground in the upright posture, thus freeing the hand for constructive and acquisitive purposes, called upon the brain for its supreme development in the parietal lobe.

Simultaneous with the expansion in kinesthetic sensibility, the motor areas of the cerebral cortex have enlarged. By their extension they have increased their capacity for the creation of more numerous and varied motor patterns. They have gradually developed all of the motor formulae essential to the almost innumerable skilled manipulations of human hands. Much emphasis has been laid upon the expansion of the sensory portion of the brain, which may thus seem to play the leading rôle in development. But motor and sensory expansion have gone hand in hand. These two factors are inseparably connected. They appear to be but different phases of the same process, namely, the conversion of energy through the agency of animal organization. The stream of impulses which flows in from the outer world by the avenues of the senses is transformed into the specific energy characteristic of each form of animal life and finally transmitted to the effectors where it appears again in specifically purposive reactions. The intricacy of the apparatus for the intake and that for the output vary directly with the complexity of reaction. They are both, therefore, parts of the same energy-transforming mechanism. It is impossible to consider the sensory organization of the brain apart from the motor. This applies to all types of sensibility. The expansion in visual capacity indicated by growth in the occipital lobe supports this view. For as voluntary acts became capable of more effective performances, visual functions were increasingly more necessary to their acquisition and control. Hearing, as the instigator and guide of new motor progress, may seem to carry less responsibility than the other senses except in one transcendent particular. Auditory function made possible the recognition and imitation of the many voices of nature. It finally became the guide of motor impulses for the tongue, for the larynx, for the lips, cheeks and throat until the audible energy of the outer world was transformed into spoken sounds of the human voice. Sounds of this kind eventually assumed symbolic associations with gestures and other movements of the body, with objects seen or otherwise perceived. The inception of human speech had its structural basis in the first and second temporal convolutions whose expansion is at least indicated in pithecanthropus. These gyres represent the fundamental sensory elements of speech while the inferior frontal convolution, constituting Broca's area, exercises motor control over spoken language. All of these expansions in the several different areas of the brain are ultimately reflected in the development of the frontal lobe. The cumulative effects of many factors impress themselves upon this region. The assumption of the erect posture, the freer use of the hands, the fuller sensing of the world, the acquisition of speech and constructive proclivities, the incentive to explore and the ability to migrate, combined to broaden human experience and to increase the capacity to learn therefrom. The part they played in individualizing human personality, in expanding the powers of selection, in creating the foundations of judgment and reason is obvious. All of these higher psychic faculties are now attributed to the frontal lobe.

In the evolution of structure and behavior indicated by the brain of Pithecanthropus erectus, many factors have reacted and interacted. It is doubtless true that no single formula attempting to outline the sequence of events in this process would be wholly satisfactory or correct. Some working program of this kind, however, is not objectionable and may be helpful if its hypothetical nature is frankly admitted. The following summary of such a sequence visualizes pithecanthropus as departing from the pronograde stem of the primates and making decisive advances beyond the anthropoid stage by:

1. The development of more extensive kinesthetic and motor capacity
2. The assumption of the erect posture

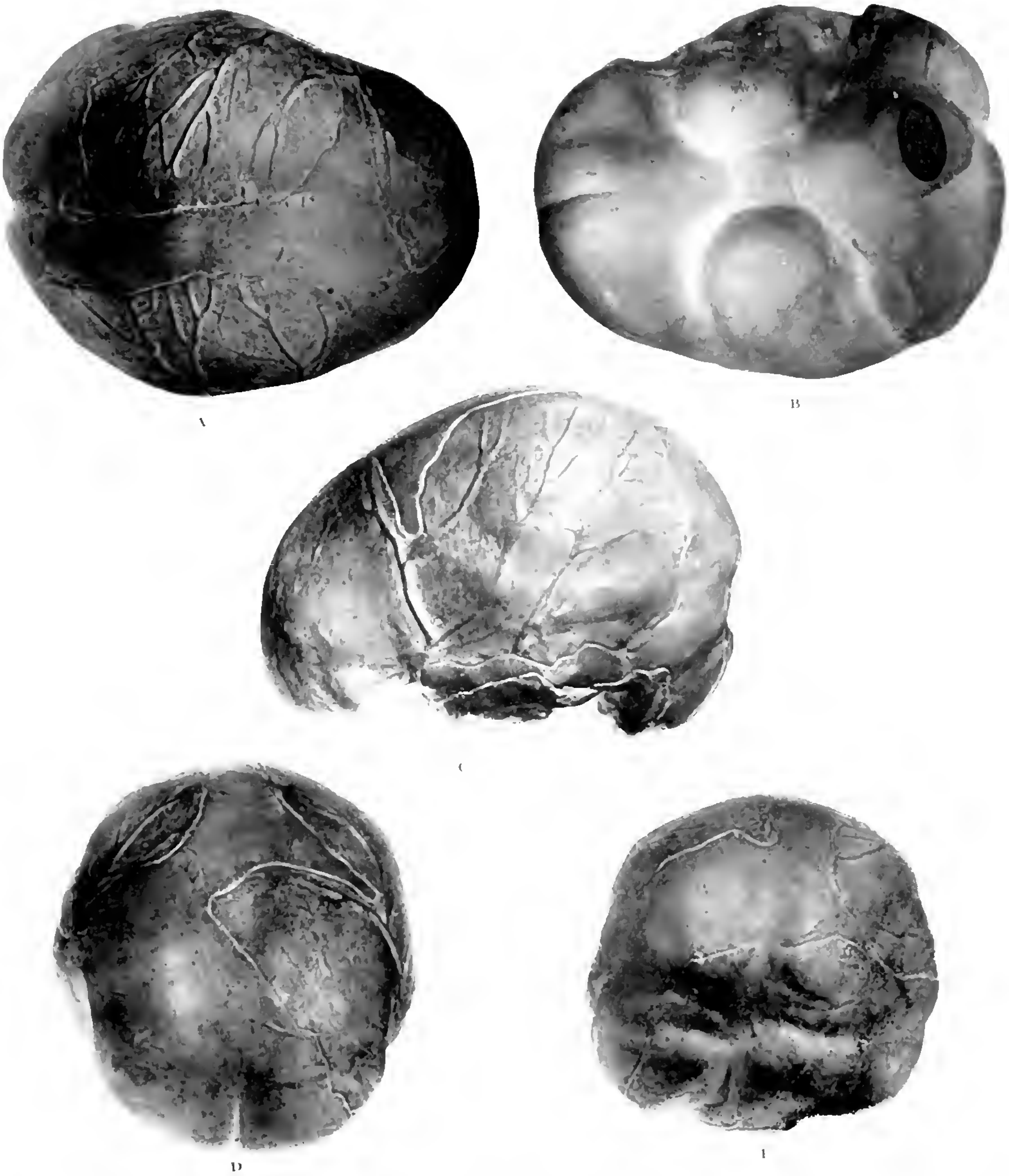
3. The freeing of the hand for manual performances and the inception of unidexterity
4. The expansion of visual and auditory sensibility
5. The development of speech
6. The establishment of human personality and the higher psychic faculties.

The Brain of the Dawn Man of Piltdown, Eoanthropus Dawsoni

The fossilized remnants of the Dawn man's skull are more fragmentary than in the case of the Javan ape-man. It was therefore necessary to give each fragment its proper place in reconstructing the skull of this long extinct race of men. These Piltdown cranial fragments include:

1. The left and part of the right parietal bone
2. The left temporal bone in its squamous, petrous and mastoid portions
3. A large part of the left half of the frontal squamosa
4. About two-thirds of the occipital bone
5. The right half of the mandible.

The first reconstruction of the Piltdown skull was presented to the Geological Society in London in December, 1912, by Sir. A. Smith Woodward, of the British Museum and Mr. Charles Dawson, a lawyer, who had made the original discovery of the fossil. The announcement of this remarkable find deeply stirred the interest of scientific circles. An unknown phase of early human existence was about to be revealed. The reconstructed skull as pieced together by Dr. Woodward impressed all who saw it as a strange blend of man and ape. It seemed that the missing link for which the early followers of Darwin had arduously searched was at length forthcoming. But whether this was the long sought missing form or not, the Piltdown strata in the Weald of Sussex, not many miles from the English Channel, told of a race



FIGS. 376 TO 380. FIVE VIEWS OF THE ENDOCRANIAL CAST OF EOANTHROPUS DAWSONI (DAWN MAN OF PILTDOWN). CONSERVATIVE ESTIMATES GIVE THIS FOSSIL AN ANTIQUITY OF 140,000 YEARS. IT IS PROBABLY MUCH MORE ANCIENT. RESTORATION BY PROF. J. H. MCGREGOR.

(A) Vertex, (B) Base, (C) Left Lateral Surface, (D) Frontal Pole, (E) Occipital Pole. The smoother areas in the cast show the regions which have been restored.

of human beings who inhabited England long before history had made its feeblest beginnings. The stratum in which the Piltdown fossil rested indicated an antiquity, according to Dr. Woodward, dating back to the early part of the Pleistocene period. The estimates of this geological period in terms of years vary considerably. Such authorities as Professor Sollas and Professor Penck, for example, believe the period comprised between 400,000 and 500,000 years. Professor Rutot is more conservative and sets the figure at 140,000 years. Sir Arthur Keith, who made a subsequent reconstruction of the Piltdown skull, advocates an antiquity even more remote, dating back to some portion of the Pliocene. Even if it is impossible to be more exact in these estimations of geological time, it seems clear that a very primitive race inhabited England long before Caesar's invasions; in fact, ages before the ancient Britons claimed the land which was destined to produce the most brilliant lights of history.

Endocranial casts of the Piltdown skull have been made by Dr. Woodward and Sir Arthur Keith. These reproductions vary in certain details, particularly in regard to the arch of the vertex and the estimated volume of the brain. Both of the casts show a distinct superiority when compared with that of pithecanthropus (Fig. 366). Especially decisive is the gain made by the Dawn man in the vault of his skull and the expanse of his forehead. The general flatness in the cranial vault of the Javan ape-man gives place to a degree of arching in the Piltdown skull. This modification is in response to expansions in the frontal and parietal regions. But increasing proportions are not limited to these areas. The temporal as well as the occipital lobe of the Dawn man have enlarged. By comparison it is evident that the brain of the ape-man was smaller, less well developed and less specialized. The volume of the pithecanthropus brain, as originally estimated by Dubois, was 855 c.c. Subsequent measurements with corrections by McGregor place this figure at 940 c.c. This brain volume, while considerably above the average for the gorilla, which is between 500 and 545 c.c., is much below the average adult human brain of modern races. Professor Elliot Smith maintains that a brain must reach the weight of 955 gms. (about 1000 c.c.) before it can serve the ordinary needs of human existence. Woodward eventually estimated the volume of the Piltdown brain at 1195 c.c., but Keith's investigation increased this figure to approximately 1400 c.c., or well up to the average of the modern man. The gorilla's brain volume appears to be 57 per cent that of pithecanthropus, while pithecanthropus is about 72 per cent of the Piltdown brain volume. This difference denotes more rapid brain expansion in the direction of the higher human standard, once the limits of actual anthropoid conditions are transcended. The impetus toward human specializations, even in their early human incipiency, seems to hasten the progressive development of the brain more than any of the less advanced primate stages. Some of the increase in the brain volume of most primates might be attributed to general increase in body structure. Such, however, can scarcely be the case, since a gorilla weighing nearly four hundred pounds, or more than twice as much as the average man, possessed a brain whose volume was only 545 c.c., approximately one-third that of man. Dubois and Keith endeavored to determine how much of the brain is needed for purely animal contingencies and size of body. They concluded that these factors are represented by not more than 6 per cent to 8 per cent of the entire cerebrum. Between 92 per cent and 94 per cent of the volume of the human brain is therefore determined by other factors than the vital functions or the size of body.

The surfaces of the Piltdown endocranial cast are shown in Figures 376–380.

THREE SALIENT LANDMARKS ON THE PILTDOWN ENDOCRANIAL CAST

Three salient landmarks on the cast are, all things considered, less impressive than in pithecanthropus. The fissure of Sylvius may be discerned at the frontotemporal notch where its posterior limb begins to pass backward beneath the parietal eminence. The termination and ultimate disposition of this fissure cannot be determined. It presents a faintly indicated anterior ascending ramus and also a horizontal ramus extending into the frontal lobe. The position of the Rolandic fissure may be estimated by the general rules previously applied to this sulcus in the pithecanthropus brain. The groove of the transverse sinus is well defined but seems open to considerable criticism, especially concerning its obliquity as given in the endocranial cast. As a whole, the occipito-cerebellar area is the least satisfactory region of the entire cast. Subsequent studies may correct this deficiency and produce an occipital symmetry more in keeping with this portion of the normal skull.

THE FRONTAL LOBE OF THE DAWN MAN

The frontal lobe of the Dawn man presents much less in the way of frontal impressions and juga than pithecanthropus. It offers no more convincing indications as to the position of the Rolandic fissure. The coronal constriction is much less marked than in the Javan man, thus showing a real expansion in the frontal lobe. In one feature this area does stand out by comparison. The inferior frontal convolution of the Piltdown brain is much more prominent than in pithecanthropus. In it are apparent those extensions of the Sylvian fissure so notable in connection with the motor speech area of Homo sapiens (Fig. 381). The increased size of the frontal lobe, together with the augmented prominence of Broca's speech area, is no doubt indicative of a human being endowed with better linguistic abilities, broader capacities for experience and improved reasoning powers. There is little to denote expansion in the motor area or in the intermediate precentral area for skilled movements. One clue to the probable extensions in these important regions is furnished, however, by the parietal lobe which may now be considered.

THE PARIETAL LOBE OF THE DAWN MAN

The parietal lobe, although it lacks any impression of fissures or convolutions, has evidently increased in size. This is especially noticeable in the parietal eminence and in the prominence of the arc of the vertex. Both of these increments signify accessions to general body sense and are incident to specific expansions in the area pertaining to the upper extremity, more especially the hand. Such augmentation of the parietal lobe justifies the interpretation of further extension in manual attainments. There is reason to believe that the Dawn man had acquired increased capacity in the use of his hand as a sensory organ. He could employ it to much advantage in exploring the world about him, and in analyzing the objects in his environment by actual contact with them. Thus he learned the consistency, the shape and the texture of things he touched. The weight and mobility of objects gave him added information concerning their utility and application. The relative resistance of wood and stone, their respective projectile and penetrating powers, the advantages of sharp edges as compared with blunt surfaces, the pliability of flexible substances, the tensile strength of various tissues, all came to him as revelations called forth by these new perceptions of the world. But such revelation did not limit itself to mere sensing. The sensory impressions found externalization in new actions. They doubtless guided his hand to utilize the serviceable qualities of objects with which nature surrounded him. In a word, they led him to make use of stick and stone, from which advance it was but a step to fashion his materials into implements better suited to his purposes.

While the increase in the parietal arc and in the parietal eminence denotes new capacities of sensation, it is quite as insistent concerning the motor powers added to the human hand. There may be a question whether the earlier ape-man of Java had learned the secret of making implements for himself, but it is becoming more clear that the crude flints found in the same stratum with the Piltdown skull were the production of human skill. These eoliths have occasioned much debate concerning their "humanity." If it should at length be decided that they formed no part of the Dawn

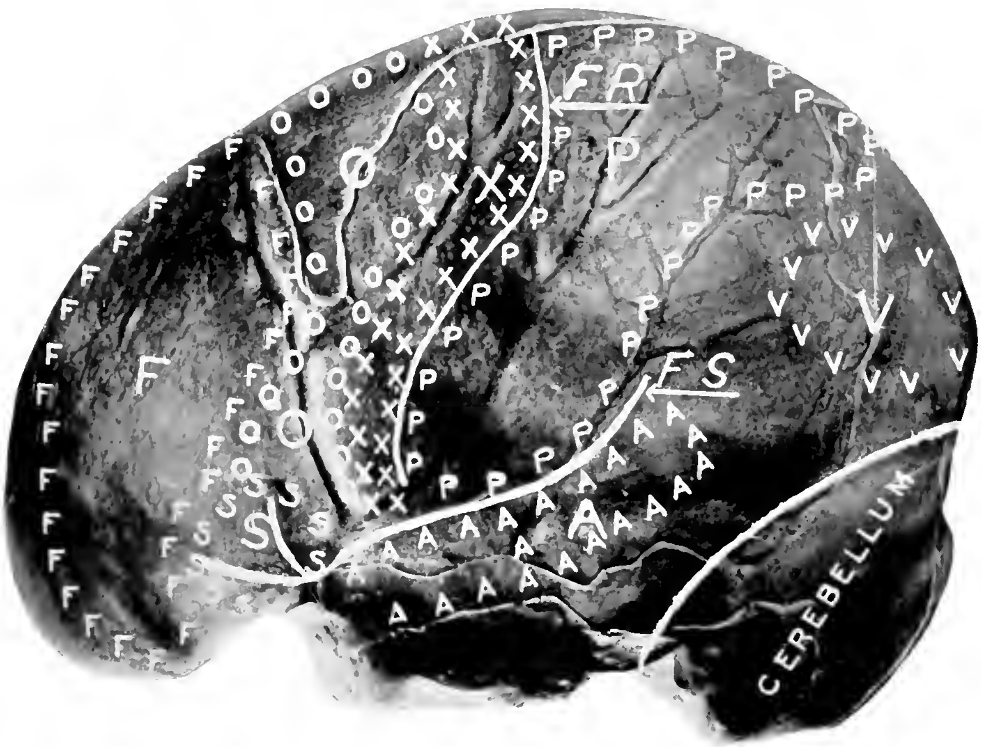


FIG. 381. FUNCTIONAL LOCALIZATION OF THE BRAIN OUTLINED UPON THE LEFT HEMISPHERE OF THE ENDOCRANIAL CAST OF EOANTHROPUS (PILTDOWN). RESTORATION BY PROF. J. H. MCGREGOR.

A, Auditory Area; F, Higher Faculties; FR, Fissure of Rolando; FS, Fissure of Sylvius; O, Area of Skilled Movements; P, Sensory Area; S, Speech Area; V, Visual Area; X, Area of Voluntary Motor Control.

man's equipment, the development of his brain does not gainsay his ability to manufacture or use such implements. This is all the more true since the slightly larger size of his left hemisphere plainly suggests unidexterity. The chipping of flint instruments, above all other activities, would require such a modification in his manual organization that one hand served to hold and the other to shape the flint.

To explain the increased dimensions characteristic of the Piltdown brain, it seems necessary to presume that this race had made certain adaptations which called for added neural capacities. In all the varied adaptive radiations seen in other mammals, there is no demand for complex adjustments comparable to that affecting mankind. Search as one may amongst all of these variations, no influence, no single factor appears so compelling of cerebral specialization as the development of the human hand. By this means an entirely new world had been laid open for man to conquer, and a still newer one waited for him to construct. So it was that a brain sufficient for the simple living in plain and forest could no longer serve this new mastery of life.

The parietal lobe, although it primarily represents administration in one of the chief departments of the sensorium, also expresses the externalizing capacity of the brain. This is likewise true to a somewhat less extent of the other cerebral lobes representing the special senses.

THE TEMPORAL AND OCCIPITAL LOBES OF THE DAWN MAN

The temporal and the occipital lobes also reveal a marked advance. The casts of the Piltdown endocranium are fortunate in showing most of the left temporal lobe. The reconstruction of Dr. Woodward differs from that of Sir Arthur Keith in disclosing but little of the superior temporal convolution. Keith believes that his reproduction is in better accord with the conditions of human anatomy. His cast also obviates the marked deflection inward of the tip of this lobe and thus gives it a less simian appearance. Large portions of the middle and inferior temporal convolutions are clearly delineated, together with a part of the temporo-sphenoidal surface of this lobe. Both casts show a pronounced increase in the auditory eminence as compared with pithecanthropus. This eminence is situated at the base of the temporal lobe where the latter comes into relation with the occipito-parietal area. It represents a cortical region engaged in the sense of hearing, more particularly for complex sounds, such as those of language. In this capacity it acts as a most important component of the speech mechanism. Not only does it make possible the learning of language, but through motor reproduction of what is previously heard it provides a constant auditory supervision over language as it is vocalized in audible speech. The individual possessed of articulate expression "listens in," so to speak, while he is talking. If it is true that thought depends upon unspoken language, the auditory area of the brain exerts a profound influence over the process of thinking. The Dawn man, on the strength of these facts, must have been capable of some kind of spoken language just as he was possessed of some capacity for thought.

Little of the occipital lobe is available for study. It is difficult to determine whether the Piltdown man had better visual powers than his lower antecedents. Improvement, if there were such, involved his visuo-psychic functions, i.e., the visual powers of association and discrimination.

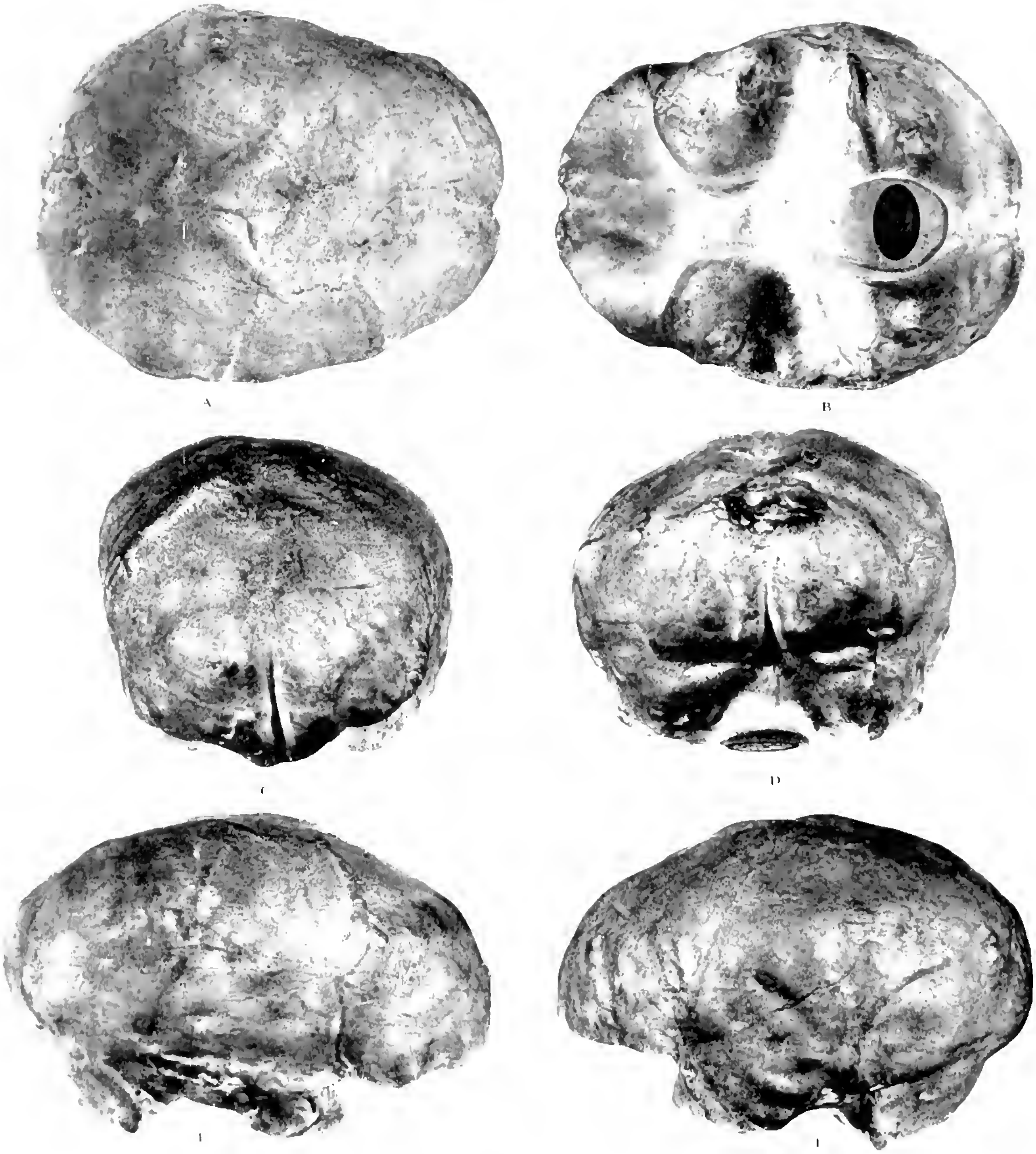
POSITION OF THE DAWN MAN IN THE HUMAN FAMILY

Thus visualized through the development of his brain, the Dawn man may appear a somewhat uncertain member of the human family. Doubtless he lived in communities of considerable size, for otherwise his powers of vocal communication would have had little opportunity to develop. He seems to have been capable of many skilled acts, but such implements as he did make were probably dictated by the bare essentials of life, by the need for food and for protection. It is probable that none of his instruments served for cultivating the soil or for the production of garments or the construction of permanent dwellings. He was dependent for his livelihood upon game animals which he followed in their migrations and thus himself became a wanderer. What powers of thought he had or what gifts of imagination are matters for conjecture. Nothing remains from which to surmise his actual customs or to suggest his attitudes toward the world as he did or did not understand it. Sir Arthur Keith says that "A survey of the convolutionary regions of the brain leads to the conclusion that we are dealing here with a simple and primitive arrangement of parts; but not so simple or so primitive as to make us wish to place the Piltdown brain in a class apart from modern human brains."

The Dawn man, as his brain attests, had come a long distance from that parting of the ways at which the human and anthropoid stocks separated. But it is equally certain that there remained a great distance yet to be traversed before such a brain could attain the development characteristic of the modern human cerebrum.

The Brain of Neanderthal Man, Homo Primigenius

Eoanthropus, as his name implies, is presumed to mark the dawn of mankind. But the full day of human existence was long in coming. Ages passed during which it seems certain that several different races of primitive men made their appearance, only to die out again. It is remarkable what slight traces of their actual image these earliest inhabitants of Europe have left. There is, however, reliable evidence of at least one such race of prehistoric Europeans, the *Neanderthals*. From their scattered fossil remains they appear to have possessed many features in common. They were of relatively short stature, probably not averaging much more than five feet three inches in height. Their limbs were powerful, their necks short and extremely muscular. What distinguished them as a race was the shape of their heads and size of their brains. The Neanderthal cranium shows a low retreating forehead and a peculiarly low dome. The head seems flattened from above downward, giving the appearance known as platycephaly (flat head). The occipital as well as the frontal portion of the skull is affected by this flattening, so that the



FIGS. 382 TO 387. SIX VIEWS OF THE ENDOCRANIAL CAST OF HOMO NEANDERTHALENSIS (LA CHAPELLE AUX SAINTS). ESTIMATED ANTIQUITY OF FOSSIL, ACCORDING TO PROFESSOR OSBORN, APPROXIMATELY 300,000 YEARS.

(A) Vertex. (B) Base Restored. (C) Frontal Pole. (D) Occipital Pole. (E) Right Lateral Surface. (F) Left Lateral Surface.

head must have been supported by a thick powerful neck, quite similar to the gorilla.

Even more conspicuous is the heavy ridge of bone above the orbits, the supraorbital torus, which produces the facial aspect familiar in the "fighting mask" of the great apes (chimpanzee and gorilla). The orbits themselves were larger than in modern man and separated by an anterior narial opening which indicates the presence of a broad flat nose. The lower jaw was heavier and broader than in Homo sapiens, although the teeth as a whole were strikingly human, having none of the fang-like specialization of the great anthropoids. On the mandible in the region of the chin there is no mental eminence. All of these cranial characters must have given the Neanderthal man a singularly gorilloid appearance. The low beetling brow, the flattened vault of the skull, the head set close upon the shoulders, the broad flat nose, the heavy jaw and receding chin could hardly fail to produce a countenance in many respects as brute-like as the great anthropoid apes. Envisaged from his fossil remains, Neanderthal man was indeed a savage-looking creature. But his brain is not altogether in keeping with this low estimate of him. In fact, the volume of the Neanderthal brain is somewhat greater than that of modern races. This cerebrum does not denote such low psychic organization as the ape-like appearance of the head would seem to suggest.

Neanderthal man had made definite advances in human progress. He laid the foundation of many customs and tendencies which later dominated social organization. He was a skilled artisan and flint worker. He had command of fire which he employed both as an invaluable accessory to his life and in the upbuilding of distinctive cultural attainments. He buried his dead with ceremonial rites, which shows at once that he believed in a future existence and possessed some religious conceptions. Far from being a lowly ape-like creature, he had many of the higher attributes of man. Although the Neanderthal had a decidedly pithecoid cast of countenance, he also displayed a human ability not to be despised. For this reason he is known as *Homo primigenius*. Yet his ape-like affiliations, in spite of his human intelligence, make it probable that he was not the direct ancestor of modern man.

FIG. 388. THE NEANDERTHAL FLINT WORKERS.

This group of Mousterian cave dwellers is taken from a mural painting by Charles R. Knight made under the direction of Professor Osborn. It is arranged to show the physical characters of Neanderthal man. The background is the famous cavern of Le Moustier. From The Hall of the Age of Man, American Museum of Natural History.

The fossil remains of the Neanderthal race have been found widely scattered throughout Europe, in France, in Belgium, in Germany, in Moravia, in Croatia, and even in the Island of Jersey. The earliest discovery of this race dates back to 1848, when the Gibraltar skull was found by Lieutenant Flint. The significance of this find, however, was not fully appreciated for more than sixty years. Neanderthal fossils comprise a collection of skulls, skeletons, mandibles and teeth in total, a remarkably large number of fossilized parts from which the osseous appearance of the race has been determined beyond all doubt. Of the skulls only four serve the purposes of exact endocranial study, such others as are known being too fragmentary or too greatly damaged to permit of more precise deductions.

In the valley of the Dordogne, southwestern France, the Abbés Bouyssonie and Bardon (Autumn, 1908) discovered in a cavern near the little village of La Chapelle aux Saints, the skeleton of a primitive man. The body rested upon its back with its head toward the west, its legs, thighs and forearms flexed. The head had been especially protected by flat stones and many skillfully worked flints of the Mousterian period surrounded the skeleton. There was every evidence of interment and burial ceremony about this discovery. Professor Boule of the National Museum of Natural History in Paris concluded that the skeleton was that of a man about middle age, belonging to the Neanderthal race. In its dimensions the skull exceeds those of an average modern man, having the exceptional capacity of 1600 c.c., which is at least 120 c.c. above the modern average. But the skull was distinctly low vaulted and had an ape-like supraorbital torus with low receding brow. The endocranial cast of the La Chapelle man serves especially well to give us an accurate view of the Neanderthal brain (Figs. 382 to 387).

FEATURES EVIDENT IN THE CAST OF THE NEANDERTHAL SKULL FROM LA CHAPELLE AUX SAINTS

This cast shows those features which might be presumed from the Neanderthal skull. The shape of the brain is distinctly flat. That arching in the region of the vertex so prominent in Homo sapiens and at least slightly foreshadowed in the brain of pithecanthropus, as well as in the Dawn man of Piltdown, is remarkably absent. In a portion of this arc which affects the prefrontal region, the curve actually seems to sink inward. With all proper allowances for discrepancy in reconstruction, it is nevertheless certain that the vertical areas of this brain have adapted themselves to a flattened head. This observation is particularly pertinent from the fact that it is the brain which in the main appears to determine the shape of the skull. Doubtless there is an interplay of factors in this growth relation, but the cerebrum is the essential organ of the cranium and its developmental demands are of chief moment during the important formative period. It is the shape of the brain rather than the shape of the head which may be considered a determining character in the Neanderthal race. In its shape, this brain is far from ape-like. It bears all the marks and features of the human cerebrum.

Certain intrinsic factors in cerebral development may conceivably be related to the brain flatness of the Neanderthal. Thus, for example, the ventral horn and body of the lateral ventricle may be less capacious, the rhinencephalon (olfactory brain) may be more expansive, the corpus callosum less well developed, or the centrum ovale contain less medullary substance. Such modifications in the normal process of brain growth might contribute to cerebral flattening or broadening. But none of these purely conjectural possibilities seems so likely to influence development as the salient factor which plainly declares itself on the surface of the Neanderthal brain.

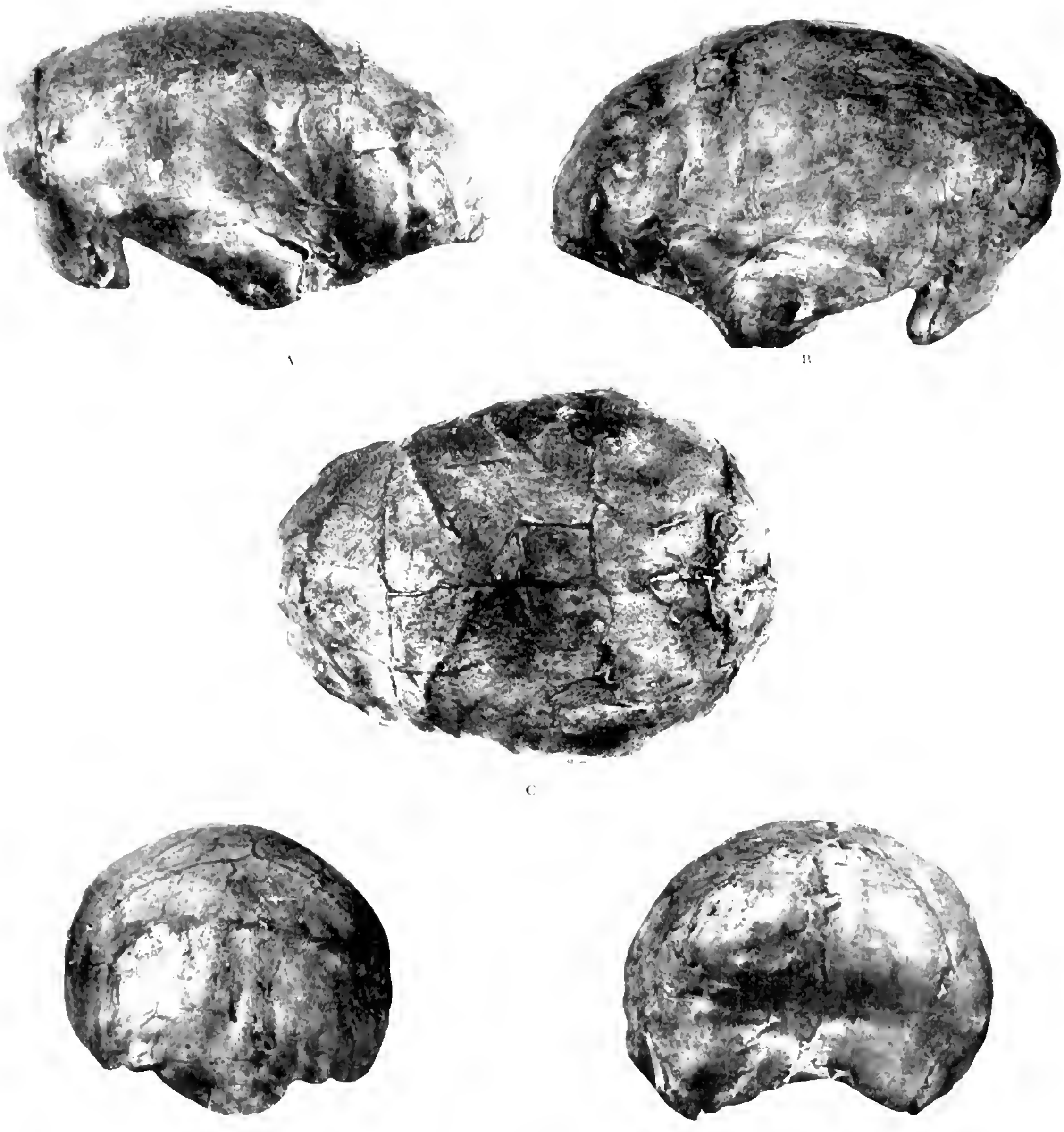
Compared with the ape-man of Java, as well as with the Dawn man, the Neanderthal possessed a brain which showed expansion in all its major divisions. The parietal, the occipital, the temporal lobes have all increased in size. So also has the frontal lobe, but the ratio of its expansion appears to be less than in the other areas. In this region the real flatness of the brain is most pronounced. Not only have the frontal convolutions on the convexity failed to give the forebrain those dominant characters which call forth the high wide forehead of modern man, but the representation of the frontal lobe on the mesial surface appears to have remained in its more primitive state. Certain secondary effects leading to the flattened aspect of the brain would of necessity follow in this connection, and still further emphasize the low vaulting of the brain. A lagging development in the frontal lobe would determine a centrum ovale of relatively small dimensions because of smaller fiber contributions from the corpus callosum and from adjacent association areas. The rostrum and body of the corpus callosum would in consequence be smaller, and thus fail to furnish that fractional increment which gives the complete fullness to the frontal arc in Homo sapiens. This apparent failure of the Neanderthal frontal lobe to attain its ultimate proportions not only characterizes the organ from a structural point of view, but must have had a far-reaching influence upon the ethnical cultures and final destiny of these primitive Europeans.

The Sylvian Fissure. The position of the Sylvian fissure is readily identified in its posterior division extending from the fronto-temporal notch beneath and caudal to the parietal eminence. The arrangement of its caudal extremity is not discernible but its anterior and horizontal rami are clearly defined.

The Fissure of Rolando. The fissure of Rolando may be introduced on the basis of the usual estimations for this sulcus. Its exact position, length, angle of inclination, and terminations are mainly hypothetical since no actual groove on the cast indicates the presence of the fissure.

The Transverse Sinus. The groove of the transverse sinus is visible and marks the division between the cerebral hemispheres and the cerebellum.

The Frontal Lobe. The frontal lobe as a whole bears evidence of much expansion as shown by the broadening of its pole and a tendency to round out the arc, which gives the identifying prominence to the modern forehead. The process, however, involves only the polar areas of the lobe in which the impressions of the superior and middle frontal convolutions are apparent. In the remainder of the frontal area there is no sign of fissures or convolutions. The exact allocation of precentral motor area or of the intermediate precentral area for skilled movements cannot be made. The coronal constriction is quite conspicuous. A large Pacchionian elevation is situated near the superior longitudinal fissure in the line of the coronal suture. Upon the right hemisphere the position of the middle meningeal artery is faintly visible, while upon the left it is less distinct. The outstanding feature of the frontal lobe is the prominence of the inferior frontal convolution. This



FIGS. 389 TO 393. FIVE VIEWS OF THE ENDOCRANIAL CAST OF THE LA QUINA SKULL. (NEANDERTHAL WOMAN.)

(A) Right Lateral Surface. (B) Left Lateral Surface. (C) Vertex. (D) Frontal Pole. (E) Occipital Pole.

gyre on the left side is more complex in its arrangement than in either the Javan or Piltdown man. In it may be recognized the pars orbitalis, the pars triangularis and the pars basalis, all characteristic features of Broca's speech area in Homo sapiens (Fig. 400).

Such frontal development is indicative of psychic powers in advance of the still more primitive races of man and also of a capacity for speech which seems to be approaching modern standards. Neanderthal man possessed a degree of reasoning ability and judgment which he doubtless applied with advantage to the organization of his efforts and the regulation of life. His acknowledged capacity for speech shows that his was not an existence of isolation but rather that the economic value of communal living had been appreciated and utilized. His advances in the mastery of his environment may be understood from the better development of his frontal lobe. He had come to recognize some of the elements of human superiority as compared with other living creatures. In his contests with the beasts of prey he had gained a certain degree of ascendancy, enough at least, in his later cultural periods, to dispossess his carnivorous enemies from their caverns. These shelters he took over for his own abode and thus gave the embryonic sense of ownership a new impetus. He buried his dead in a manner showing belief in a life hereafter. In such customs as these he revealed not only a fertile imagination, but that pervasive conception which in time created an egoistic superiority deemed worthy of perpetuation after death. Yet, even with all these human advances, his frontal proficiencies left something to be desired. He lived and prospered for vast periods of time but he failed to develop those qualities which guaranteed to his kind terrestrial permanency. At length another race invaded his dominions and the Neanderthal, doubtless not without a struggle, disappeared before these new people. That he was unable to cope with the invaders bespeaks some serious omission in his frontal development, an omission which the newcomers had already overcome. Defensive cooperation on a large scale, essential to successful military puissance, may well have failed the Neanderthals in their time of need. Their eventual establishment of habits incident to cave dwelling committed them to a program of simple communal life. They were hunters and nomads first of all, and tenants only by late acquisitions. Their chief interest was the quest of game. Nothing in their antiquarian relics shows that they possessed an equipment or organization suited to effective warfare. Thus their deficiencies must have been in those departments of neural development upon which higher social efficiency depends. Failing in these attributes, they at length fell victim to those who had, through better brain power especially in the frontal lobe, already attained such advantages.

The Parietal Lobe. The parietal lobe yields little evidence of its intimate details. There are no signs of fissures or convolutions. In the cast this entire lobe indicates much expansion and it seems probable that in this area the Neanderthal brain has made its greatest advances. The parietal eminence is particularly prominent and its general position denotes a region especially involved in the receipt of sensory impressions from the upper extremity. The boundaries of the lobe with the exception of the Sylvian fissure are indefinite. No actual clue is obtainable with reference to the size and complexity of the postcentral and precentral convolutions. The estimated dimensions of the parietal lobe together with the marked prominence of the parietal eminence are, however, significant. The Neanderthal brain possessed a somesthetic capacity nearly equal to modern man, and its principal specialization involves the area pertaining to the hand. Such increment in sensibility connotes a corresponding expansion in motor capacity. Perhaps it is not giving undue stress to this sensory development to maintain that Neanderthal man had made better contacts with his surroundings and had gained greater mastery over all that his hand could touch. New combinations and modifications of objects fashioned by his hands began to yield him a rich harvest of new utilities. He was beginning to take a more dominant part in creation and not the least of the factors contributing to his increasing power was the parietal lobe of the brain.

THE TEMPORAL AND OCCIPITAL LOBES. The temporal and occipital lobes both show expansion. It is obvious that the temporal lobe has lost most of that highly simian appearance occasioned by the inward deflection of its tip. It might in fact serve the needs of modern races. It is quite as large and nearly as well developed. A long palpable groove marking the fissure of Sylvius separates the temporal from the parietal area. A lesser groove parallel to the first indicates the position of the superior temporal fissure, while a short indenture localizes the middle temporal fissure. The greater portion of the temporo-sphenoidal surface is retained in the reproduction of both temporal lobes. The convolutions on the lateral and basal aspects are well marked, giving the impression of a cerebral territory of well-developed functional capacity. More convincing is the large size of the auditory eminence situated at the confluence of temporal, parietal and occipital areas. This eminence is generally accepted as part of the speech mechanism, being especially assigned to those auditory functions inherent in spoken language. Judged by this criterion in relation to Broca's area, the Neanderthal race possessed linguistic capabilities not far below the standards of Homo sapiens.

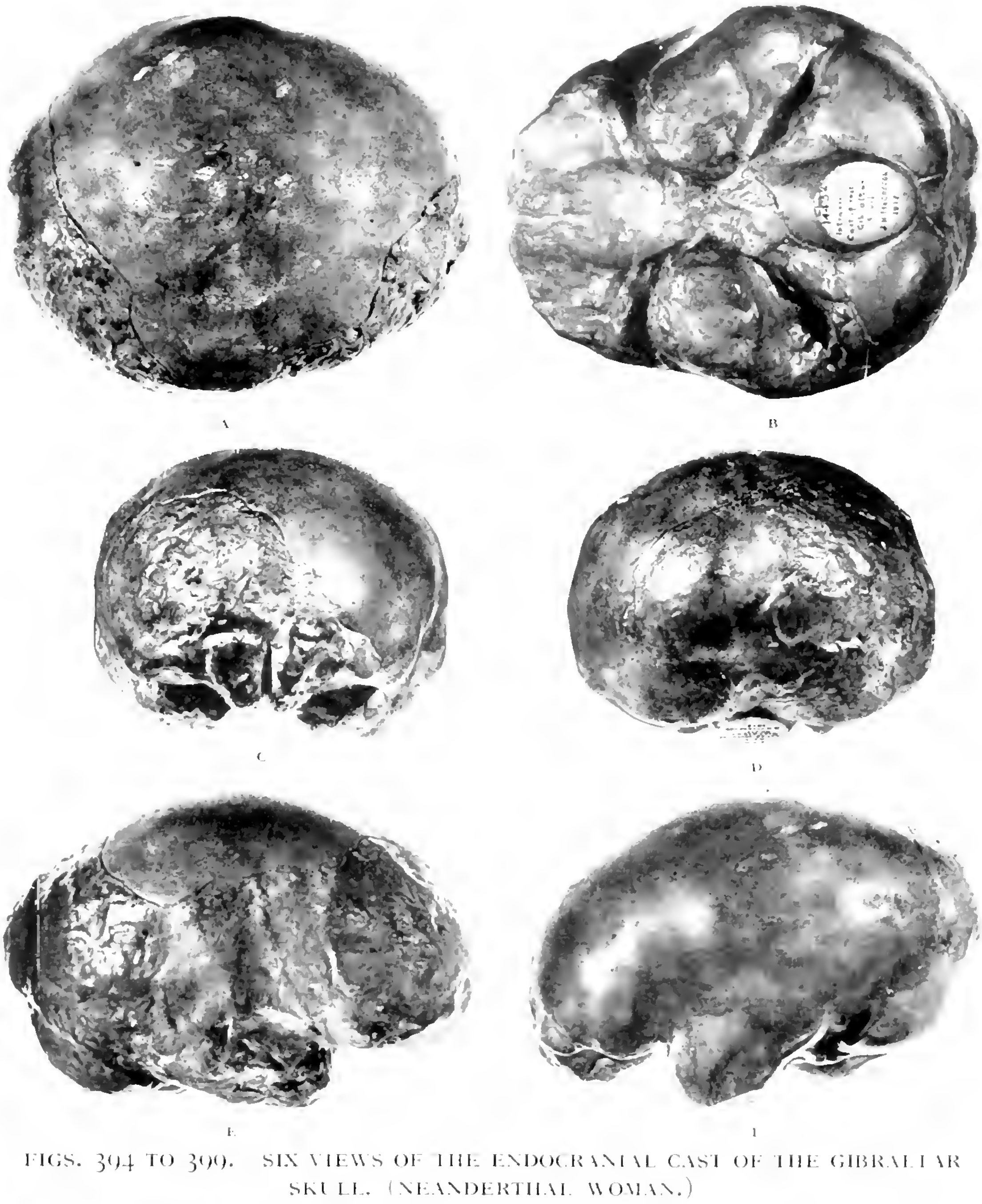
The occipital lobe also shows the effects of extensive additions. Visual function, and particularly visuo-psychic function, has been greatly expanded as compared with more primitive man. The occipital pole, as in modern races, extends considerably beyond the tentorial surface of the cerebellum. The impression of the lambdoid suture crosses this lobe transversely near its junction with the parietal area. At least one fissure, the transverse occipital sulcus, marks this lobe and separates two occipital convolutions. The lobe as a structural entity has assumed much more individuality than in the brains of lower races. It denotes a neural organization suited to more extensive visual perception and appreciation. Furthermore, it signifies the increment possessed by Neanderthal man for the visual guidance of highly organized manual skill (Fig. 400).

COMPARISON OF TWO OTHER ENDOCRANIAL CASTS WITH THE LA CHAPELLE AUX SAINTS SPECIMEN

Two other endocranial casts of the Neanderthal race should be placed in comparison with the La Chapelle aux Saints specimen. Both of these skulls are smaller and attributed to Neanderthal women.

THE LA QUINA SKULL. The La Quina skull was discovered by Dr. Henri Martin in 1911, together with other portions of the skeleton. The brain capacity, estimated by Professor Anthony to be 1350 c.c., is 250 c.c. less than that of the Neanderthal man of La Chapelle, but corresponds with other females of the race found at Gibraltar and Croatia. The cast is remarkable in two respects: It duplicates all of the cranial characters of the La Chapelle specimen with a faithfulness that compels conviction. It is, in addition, a notable example of endocranial casting. The Neanderthal peculiarities of cerebral configuration are most pronounced, as already observed, in the frontal region (Figs. 389 to 393). Here the same sharp elevation (at about 90° with the base) occurs above the supraorbital torus. It extends but a short distance and quickly falls away into the flattened arc which adapts itself to the low receding forehead. Nor is this arc consistently maintained. As in the La Chapelle cast, it sinks into an actual concavity near the plane of the coronal constriction. The entire brain seems flat partially in response to the disposition of the frontal arc, but also because of pronounced broadening in the parietal region.

The frontal lobe near its pole shows the superior and middle frontal convolutions but beyond this area there are no indications of sulci or gyres. The inferior frontal convolution is prominent in both hemispheres. In it may



FIGS. 394 TO 399. SIX VIEWS OF THE ENDOCRANIAL CAST OF THE GIBRALTAR SKULL. (NEANDERTHAL WOMAN.)

(A) Vertex. (B) Base. (C) Frontal Pole. (D) Occipital Pole. (E) Right Lateral Surface. (F) Left Lateral Surface. The smoother areas in the cast indicate the regions which have been restored.

be discerned the ascending and horizontal rami of the Sylvian fissure especially well marked on the left side. The parietal and auditory eminences are both prominent, while the occipital lobe which overhangs the cerebellum contains markings of the transverse occipital sulcus and the corresponding convolutions. The groove of the posterior ramus of the Sylvian fissure is palpable beneath the parietal eminence. Some of the temporal lobe may be defined on the lateral and temporo-sphenoidal aspects, but the outlines are less clear than in the La Chapelle cast.

The imprints of the coronal, lambdoid and sagittal sutures are particularly distinct. The course of the middle meningeal artery and its branches may be easily traced although their relief is not pronounced.

The Gibraltar Skull. The Gibraltar skull, although of greatest historical importance, does less to further our knowledge of the Neanderthal brain than those discussed in the preceding descriptions (Figs. 394 to 399). It holds its place as the premier discovery related to the existence of this race of man. A large part of this skull is missing but its reconstruction declares its Neanderthal characters. The frontal are manifests its several typical components, making certain that the brain belonged to an individual with a low receding forehead and a marked supraorbital torus. Frontal convolutions are somewhat imperfectly reproduced because of erosion in the inner table of the cranium. The parietal and auditory eminences, the occipital and temporal lobes all present Neanderthal appearances. From the purely structural point of view, the Gibraltar skull has its chief importance because it has preserved so much of the cranial base. This was a detail almost wholly missing in the other specimens. In the frontal region of the basal surface the orbital concavities are deep and much more simian than in modern races. The interorbital keels are prominent. Both of these conspicuously simian features are associated with the large orbits of the Neanderthal. The middle fossa contains the large temporal lobes and an ample optico-peduncular space. The mesial surface of the temporal lobe, near its apex, shows a well-developed uncus. The portion of the brain in contact with the middle fossa and such parts as are preserved in relation to the posterior

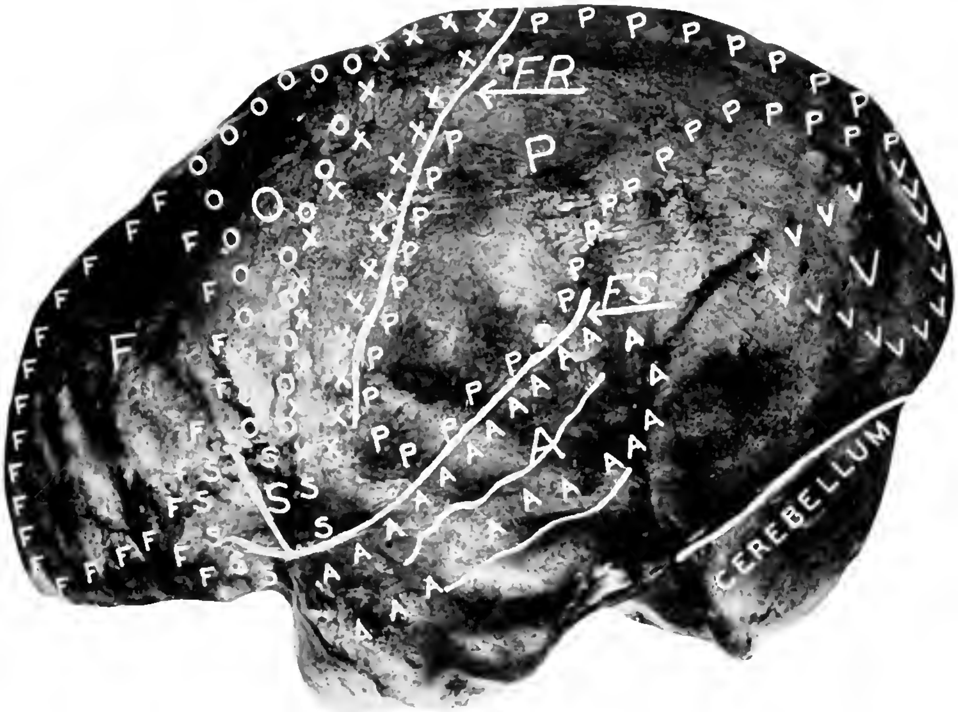


FIG. 400. FUNCTIONAL LOCALIZATION OF THE BRAIN OUTLINED UPON THE LEFT HEMISPHERE OF HOMO NEANDERTHALENSIS (LA CHAPELLE AUX SAINTS).
A, Auditory Area; F, Higher Faculties; F R, Fissure of Rolando; F S, Fissure of Sylvius; O, Area of Skilled Movements; P, Sensory Area; S, Speech Area; V, Visual Area; X, Area of Voluntary Motor Control.

cranial fossa are much more human in character than the brain areas related to the anterior fossa. This condition of affairs is remarkable and worthy of some comment.

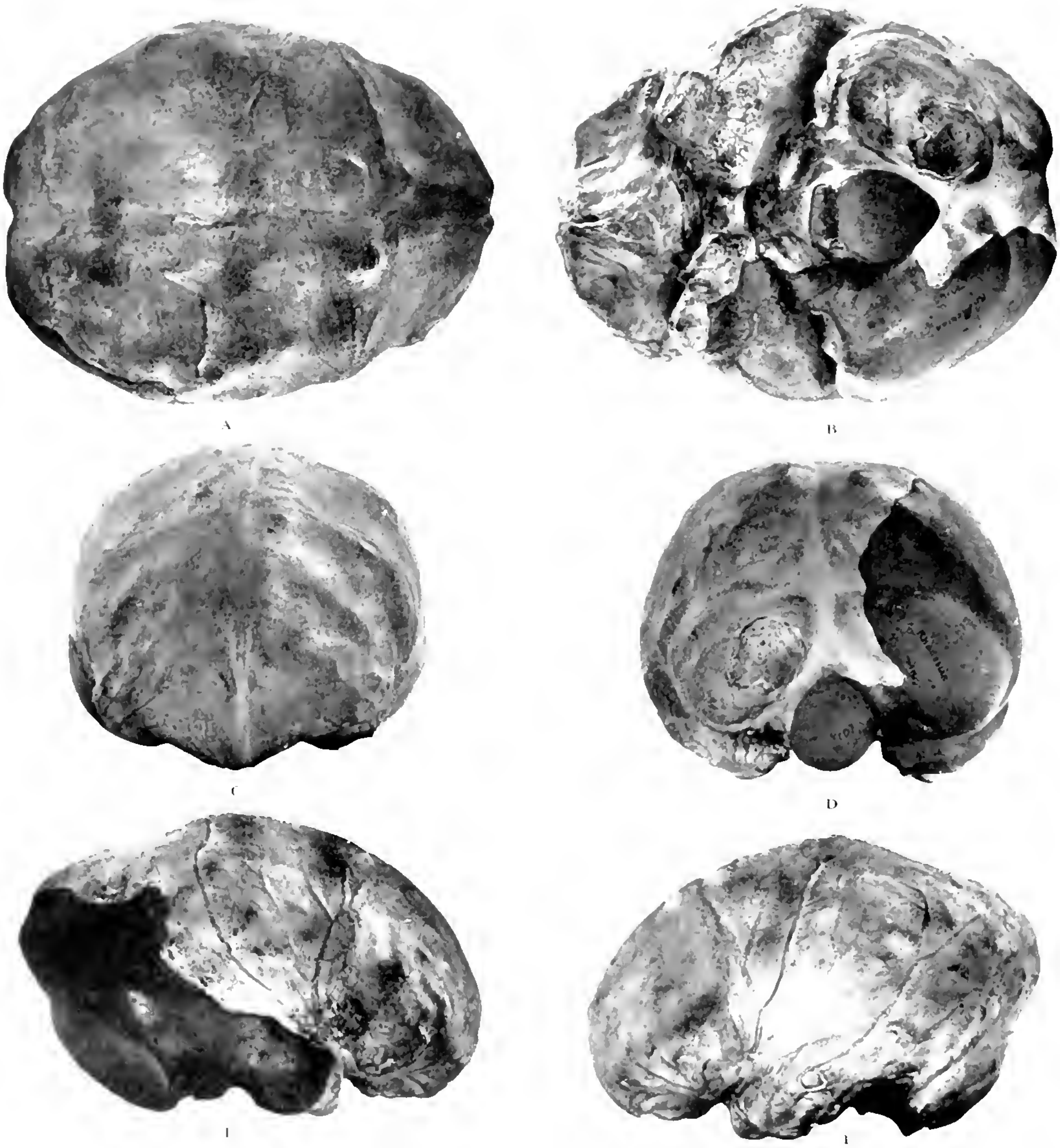
In the frontal region of the Neanderthal cranium it is apparent that certain anthropoid tendencies have had the upper hand. The capacious orbits, the heavy supraorbital torus, the low receding brow, the broad anterior narial opening impart a definitely gorilla-like appearance to the head and face. But back of all this is a region of the brain which still retains many resemblances to the great apes. Thus the orbital concavities, the supraorbital keels and the flattened frontal are are reminiscent of gorilla and chimpanzee. In this light it might seem that the Neanderthal brain was not yet highly human. It has made certain great strides in this direction, but mere increase in volume, pronounced though it may be, is not sufficient to produce the cerebral characters of the fully developed human species. One indispensable item must still be added to complete the stature of man. The frontal lobe should acquire all of those characters peculiar to Homo sapiens. A brain not so developed does not attain its full human measure. In such development cerebral growth is dominant. As the brain grows, the orbital plates flatten and the supraorbital torus recedes. In the end the pithecoid visage gradually fades until it loses its brute-like features. It does so because the frontal lobes of the brain, those last gifts of evolutional progression, have enlarged and thus compelled the humanity of man to appear in his face and head. Such a view seems also to reconcile the perplexing discrepancy between the ape-like head and man-like brain of the Neanderthal. It shows that these parts of the body are actually in harmony one with the other. It may even offer the explanation of why the Neanderthal race progressed so slowly during the passage of more than 200,000 years and at length was completely replaced by a more exalted type of man possessed of well-developed frontal lobes.

The cultural phases attributed to the Neanderthals include their feeble beginnings in the Chellean period, their advances in manual dexterity to the Acheulean era and their culminating refinements in design and execution during the Mousterian period. But these people began as nomadic hunters and so, with very slight and perhaps incidental modifications, they ended. Succumbing to the invasion of the more effective Cro-Magnons, they left no trace of themselves among this greater race. Such complete disappearance with no evidence of that interbreeding common between victors and vanquished may also be due to the Neanderthal's ape-like specializations. Racial discrimination on the basis of such wide morphological differences would tend more toward the extermination of the inferior race than to its subjugation.

THE BRAIN OF HOMO RHODESIENSIS

Asia and Europe have both produced evidence of prehistoric man, the latter most abundantly. Until quite recently Africa has been peculiarly silent in this regard. But at length even the Dark Continent has revealed signs which show that man of most primitive type had penetrated a long way into the south during his wanderings over the earth. This important discovery was made in Rhodesia and first publicly reported in 1921 by Mr. William L. Harris (*Sunday Times*, Johannesburg, Sept. 25).

The conditions under which the discovery was made were peculiar and significant. Actual remains of two human skeletons were found at Broken Hill Mine, in northern Rhodesia. These remains differed from similar fossil discoveries in one essential detail. They were not fossilized in the ordinary sense. Connected with the Broken Hill Mine there was originally a natural cave about one hundred and twenty feet long. This was known as the "Bone Cave" because it contained a vast number of animal bones all of which were so thoroughly impregnated with salts of zinc and lead as to make smelting of them worth while. At the bottom of this cave the human remains were found. Like all of the other bones in this enormous osseous deposit, the surfaces of the human skeletons were incrusted by zinc and lead so that the action of the earth had failed to mineralize the deeper bony tissue. Paleontologists accept such remains as "fossils," but unfortunately this surface incrustation precludes any estimation of the geological age of the bones. Unfortunate also is the fact that the osseous remains of animals found with the human skeletons were all of species still extant in Africa. The cave seems to have been an ancient feasting place for hyenas which dragged thither



FIGS. 401 TO 406. SIX VIEWS OF THE ENDOCRANIAL CAST OF HOMO RHODESIENSIS (RHODESIAN MAN). ESTIMATED ANTIQUITY ABOUT EQUAL TO THAT OF THE NEANDERTHAL RACE, PERHAPS EVEN OLDER.

(A) Vertex, (B) Base, (C) Frontal Pole, (D) Occipital Pole, (E) Right Lateral Surface, (F) Left Lateral Surface. The smoother areas in the cast indicate the regions which have been restored.

their prey. There is even some remote suspicion that the human remains may have come to their last resting place in the Bone Cave in a similar manner. A cleft in the roof of the cave near its far end, where a human skull was discovered, suggests the possibility that the men or women whose bones were found may have fallen into the cavern in relatively recent times.

Three important details usually helpful in the chronological assignment of human fossils were wanting in connection with these Rhodesian relics: (1) the actual fossilization of the bones; (2) the presence of extinct mammals or other animals; (3) the existence of stratifigraphic identifications. No inference may be drawn concerning the exact nature of this human depository. It may have been either accidental or the result of a burial ceremony. Furthermore, little evidence, such as the collateral discovery of paleolithic implements, may be adduced to shed light on the antiquity of the Rhodesian man. Yet, certain features, especially of the skull, have convinced eminent authorities of the great age and specificity of this race. Elliot Smith, for example, believes that the Rhodesian man is "a long lost and strangely exotic cousin" of the human family circle. He bases his opinion on the striking peculiarities of the Rhodesian face which he calls the most primitive in all the genus Homo. This face is also more brutal than that of any known human being, living or extinct. Its enormous eyebrow ridges are bigger even than those of the most archaic human, the Javan ape-man, and recall the conditions seen in gorilla. There is no indication of a groove at the side of the nose marking the boundary between it and the face, such as is constant in all races of modern man, even in the Negro, Mongol and Australian types. The merging of the nose with the face to form what in other animals is called a snout and regarded as a peculiarly significant mark of the beast is known only in one other extinct member of the human family, i.e., Neanderthal man. But the Rhodesian's nose is even more ape-like than that of the Neanderthal. Another remarkable feature of the facial skeleton is the great size of the palate and teeth, although the canines do not project in the characteristic simian manner as in the Dawn man of Piltdown or the fossilized proto-Australian of Talgai. The form of the brain case and the distinctive features of the brain alike corroborate the inferences drawn from the face which declare the Rhodesian species the most primitive of the entire genus Homo, older and more primitive in fact than Neanderthal man. The shin bone and fragment of the femur support this estimation of Rhodesian antiquity. Such is Elliot Smith's view concerning the age of this last discovered member of the human race. There is, he admits, much that is tentative about his present opinion. The Rhodesian fossils were under the charge of Dr. Smith Woodward in the Natural History Department of the British Museum at South Kensington. Dr. Woodward has already expressed his view that Homo rhodesiensis represents a phase of evolution later than the Neanderthal type. Doubtless in due time a more intensive study of these fossil remains will give a greater degree of finality concerning the antiquity of this race of primitive men.

FEATURES OF THE ENDOCRANIAL CAST OF THE RHODESIAN SKULL

The endocranial cast of the Rhodesian skull presents certain interesting and at the same time perplexing features. At first glance it seems to conform in type with Homo sapiens. Closer inspection, however, occasions considerable doubt in this regard. On the other hand, the Rhodesian brain appears much superior to that of either the Javan or Piltdown man. It is more primitive in some particulars than the Neanderthal cerebrum. Its volume is slightly larger than that of the Piltdown brain, but distinctly smaller than the Neanderthal. It has much less of the flattening in the frontal are than is true of pithecanthropus, eoanthropus or Homo primigenius. In a word, it would be difficult to associate this brain genetically with that of any of the primitive races already considered. It is, nevertheless, too small and too little specialized in certain areas to consider it in close relation to Homo sapiens. For the present it seems desirable to regard this specimen as representing a distinct race whose affinities and antiquity may be estimated in the most general terms only.

The Sylvian fissure may be located without difficulty by the deep groove starting at the temporo-frontal notch and extending backward beneath the parietal eminence. The fissure of Rolando has been introduced in the cast by utilizing the usual formula for this sulcus. The groove of the transverse sinus is well defined as are also the ridges marking the distribution of the middle meningeal arteries of the right and left hemispheres. With the recognition of such landmarks it is possible to identify the boundaries of the major lobes upon the convexity of the hemisphere although no actual limits may be defined between the occipital and parietal areas (Figs. 401 to 406).

The Frontal Lobe. The frontal lobe shows a notable absence of convolutional impressions. This is particularly true of the prefrontal area where the polar extremities of the middle and superior frontal convolutions are usually well marked. A pronounced ridge indicates the position of the coronal suture in the immediate vicinity of which are two prominent Pacchionian elevations, one on either side of the sagittal line. The frontal arc is higher than in Neanderthal man and suggests a more modern type of forehead. It does not present any tendency toward concavity in its entire extent. The frontal and intermediate precentral areas, on the other hand, show a distinct flatness indicative of a relatively incomplete development in these two regions. Two distinct areas of compression appear on either side of the coronal ridge. These are the flattened regions referred to as indicating a lack of fullness in the frontal contour. They are symmetrical in the two hemispheres and for this reason less likely to be in the nature of artefacts. The more anterior of these two depressions is included in a well-defined coronal constriction. There is no surface feature to denote any particular prominence of the precentral convolution nor of the intermediate precentral area of skilled movements. The inferior frontal convolution, however, is a conspicuous feature of the frontal lobe. It shows a considerable degree of

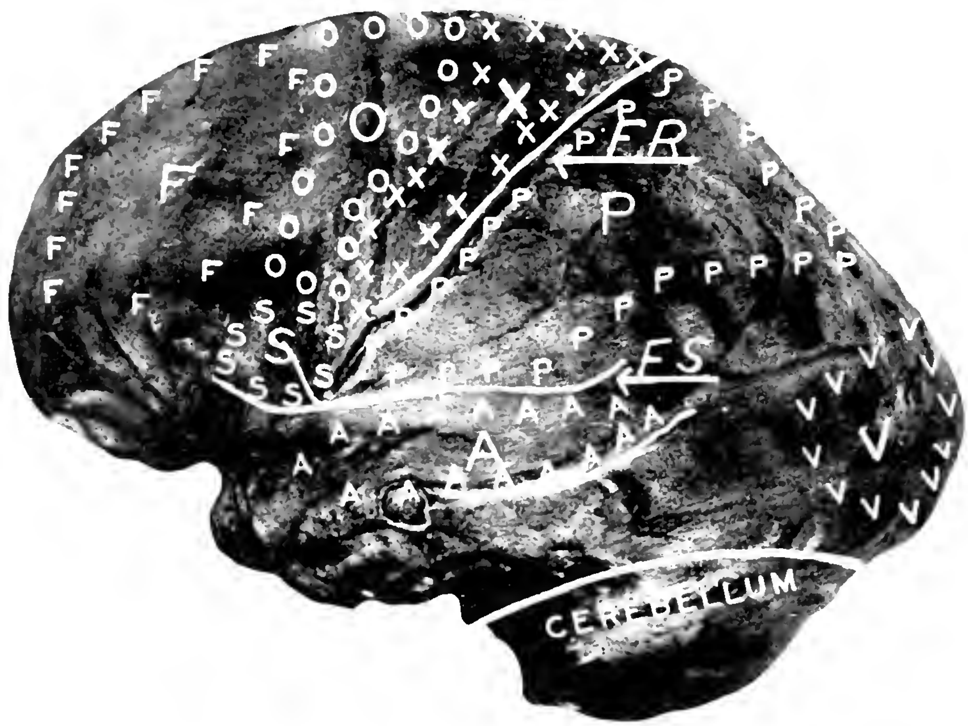


FIG. 407. FUNCTIONAL LOCALIZATION OF THE BRAIN OUTLINED UPON THE LEFT HEMISPHERE OF HOMO RHODESIENSIS.

A, Auditory Area; F, Higher Faculties; FR, Fissure of Rolando; FS, Fissure of Sylvius; O, Area of Skilled Movements; P, Sensory Area; S, Speech Area; V, Visual Area; X, Area of Voluntary Motor Control.

specialization on the left side in which the horizontal ramus of the Sylvian fissure may be discerned. The development of this convolution on the right side is almost as much advanced. The basal surface of the frontal lobe confirms the impression that this is a primitive type of cerebral organization. The orbital concavities have a simian depth and the interorbital keels are correspondingly pronounced. The imprint of the orbital convolutions is unusually prominent. In character they resemble these structures in the human brain.

By all the signs of his frontal lobe, Rhodesian man must have been a very humble sort of human. Nothing in this region of his brain denotes any approach to the attainments of Homo sapiens. The frontal area bears many marks of his simian retentions, although it also shows that his cerebral capacities had already transcended the anthropoid limits and were fast carrying him toward broader planes of human experience. It would be surprising, however, to find him capable of any advanced handicraft or productive of any such culture as characterized the Neanderthal, even in his early periods of progress. His must have been a precarious lot, pitted as he was against the formidable mammals of the African wilds. But even in this jeopardy his brain had not left him entirely destitute for the exigencies of such competition. A more facile association of ideas brought greater wariness to increase his contrivances and to amplify his strategies. He began to have a real panoramic continuity in his apperceptive life. Past experience formed the conscious background of his daily existence and entered into his plans for the future. If such advances as these may reasonably be attributed to his frontal lobe, there is evidence of a still greater advantage possessed by Rhodesian man by virtue of development in this region of his brain. His Broca's area indicates that he had acquired the powers of speech. Cooperative preparation and combined effort were thus made possible. The experience not of one individual but of many created concentrations of strength which were more than a match for the most dangerous of man's adversaries (Fig. 407).

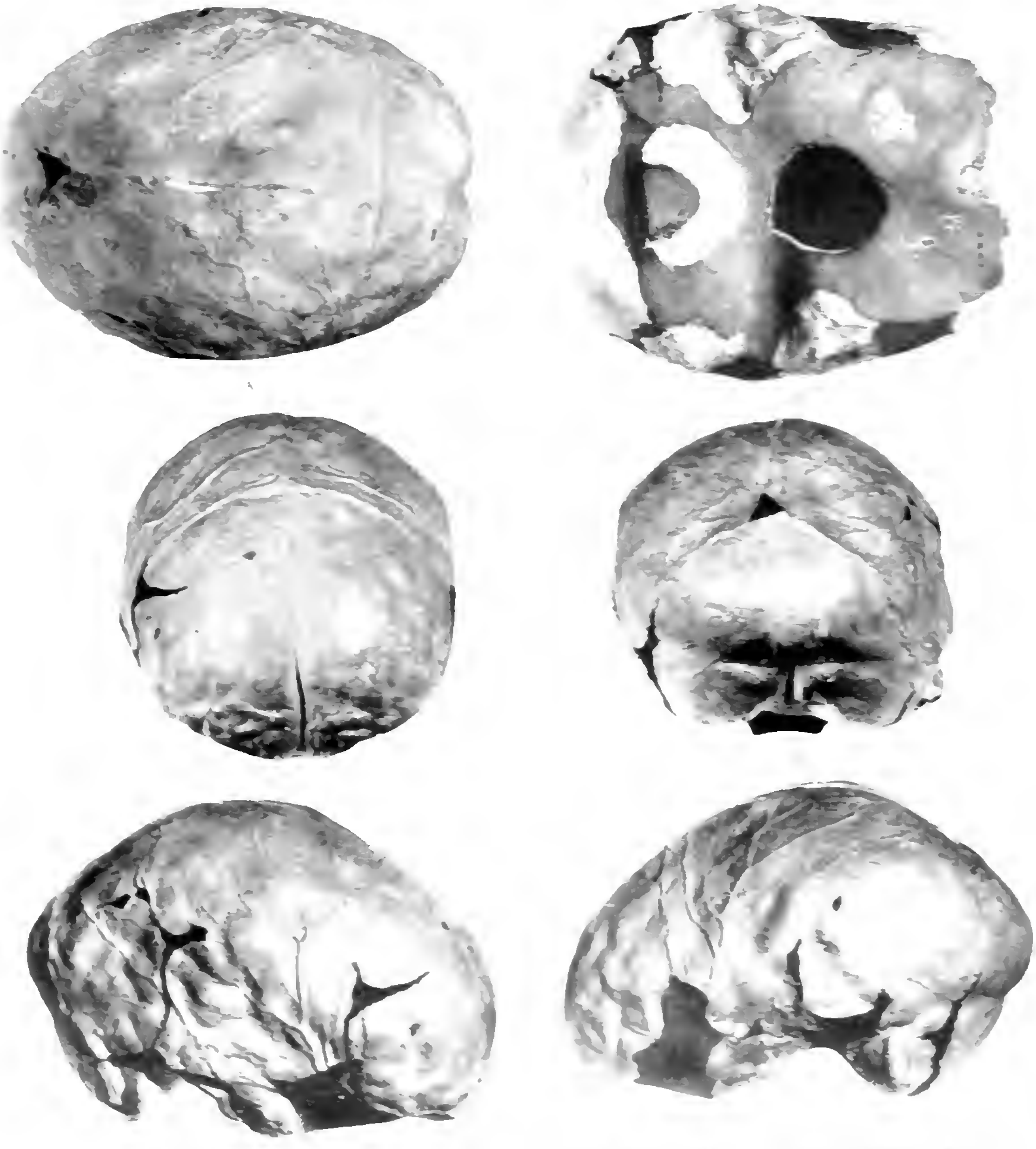
The Parietal, Temporal and Occipital Lobes. The parietal, temporal and occipital lobes indicate the extremely primitive status of the Rhodesian brain. The marked flatness which characterizes the area of the supraparietal gyrus is especially striking and significant. This region represents a functional area in which the higher elaborations of body sense are

[illegible] argument that Rhodesian man occupies a far more primitive place in [illegible] than any of the Neanderthals.

Brain of the Predmost Man

It would be particularly illuminating were the brain of the great Cro-Magnon race available for study. These people occupied an exalted position, being the earliest representatives of Homo sapiens, and the record of their remarkable existence should be correspondingly complete. But in lieu of any survey of the cerebrum of this race, it is necessary to draw analogies from certain of their human contemporaries who lived in middle Europe during Solutrean times. These others were a remarkable people also. They are known as the great mammoth hunters of Predmost whose social affiliations ally them closely to the Brünn race. The remains of these men of the Old Stone Age were found in Moravia. Associated with them were the fossilized bones of nearly nine hundred specimens of mammoths. In addition to these fossils of men and beasts there were many highly worked flints including spearheads of the laurel-leaf type, a pattern which marked this industry as that of the Solutrean era. At Predmost, where Maska discovered a collective burial of fourteen human beings, there were also the remains of six others.

In stature these people must have belonged to a large and powerful race. Their prowess as trackers of great game was exceptional, judged by the fossils of the huge mammals among which they reposed. This fact gave them the name of "mammoth hunters." But it is the reproduction of their cerebral characters which raises them at once to a plane higher than any of the earlier races of man, in fact, places them definitely in the category of Homo sapiens. These intrepid hunters had much in common with the Brünn race, much, indeed, that resembled their splendid contemporaries of western Europe, the Cro-Magnons. Of these latter there is ample record, in consequence of which they will always rank among the noblest representatives



FIGS. [illegible] SIX VIEWS OF THE [illegible]
OF THE PREDMOST RACE [illegible]
[illegible] ESTIMATED ANTIQUITY 2[illegible] YEARS

of the human species. Their remarkable artistic contributions denote far more than the executive mastery of plastic reproduction. They signalize that new spirit which had been breathed into mankind, that devotion to the beautiful in life which created an abiding enthusiasm in the race for all its highest ideals and loftiest purposes.

From earliest Aurignacian times these esthetic tendencies were dominant. It is evident in many indications of the lavish use of personal adornment, and the important rôle played by coiffure. The use of red and yellow ochre was already known, and it seems fair to assume that these pigments were sometimes used, much as in modern times, to beautify the body; perhaps also as tribal symbols and charms against kidnapping, or as tokens of war and mourning. That the Cro-Magnons had created some form of music seems almost certain. Their sketches of dances and masks made it probable that to vocal expression they had added artificial accessories in the shape of very crude musical instruments. Their art took form in mobiliary and mural reproductions. The former included movable objects bearing ornamentation on bone, ivory, horn or stone. The latter were decorations upon the walls and roofs of caverns, shelters and cliffs. Among the earliest mobiliaries are certain human statuettes and reliefs made in stone which undoubtedly represent idols. Especially noteworthy is the collection of steatopygous feminine figures carved in limestone of which the "Venus of Willendorf" has the greatest artistic merit. In their artistic discrimination these Aurignacian and Solutrean sculptors showed a decided partiality for portraying women of extreme corpulence. It was, however, in the carving of animal forms that their art reached its real heights. Many living and extinct species of mammals, birds and fish have thus been immortalized. Conspicuous among the remains of the great mammoth hunters of Predmost is a rare and undecipherable engraving on ivory. It represents a much conventionalized female figure and may have been a phallic symbol, since most of the human designs of

Aurignacian times manifest a disposition to exaggerate the sexual characters. Back of all this varied artistic creation there must have been a complex and highly differentiated social organization. Only a rich human

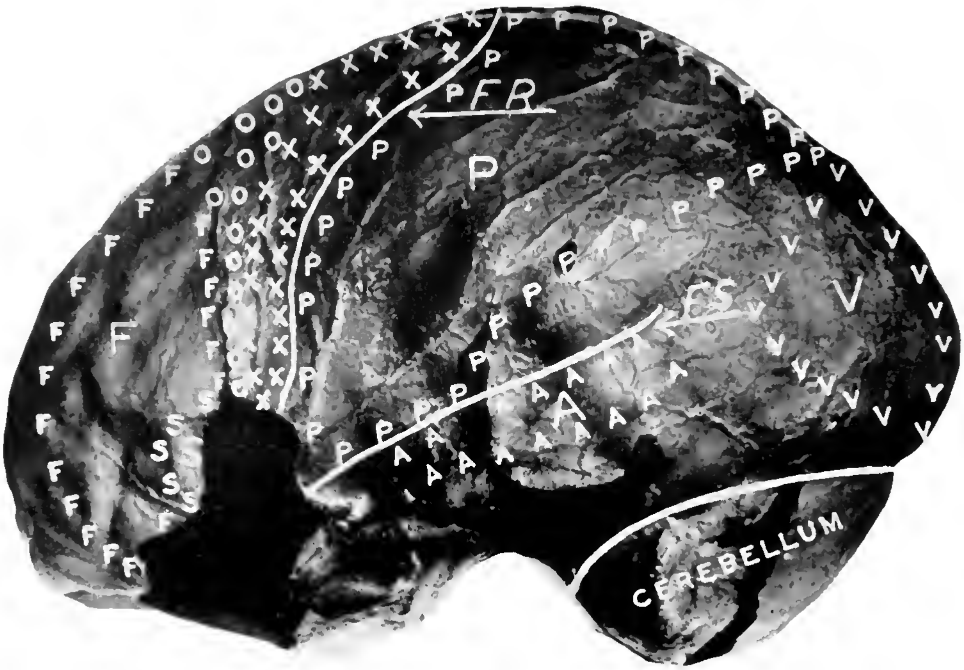


FIG. 414. FUNCTIONAL LOCALIZATION OF THE BRAIN OUTLINED UPON THE LEFT HEMISPHERE OF THE PŘEDMOST ENDOCRANIAL CAST.

A, Auditory Area; F, Higher Faculties; FR, Fissure of Rolando; FS, Fissure of Sylvius; O, Area of Skilled Movements; P, Sensory Area; S, Speech Area; V, Visual Area; X, Area of Voluntary Motor Control.

experience could provide the soil for such vivid and realistic beauty in art.

FEATURES OF THE PŘEDMOST BRAIN

The Předmost brain had made all of those essential advances which place it in the class of Homo sapiens (Figs. 408 to 413). Its volume is close to the standards for modern men. It had lost the marks of inferiority which stamp the brains of lower races of man. It had gained that refinement of structural detail which proclaims the ultimate ascendency of the human brain. The fissure of Sylvius may be easily identified and the fissure of Rolando allocated according to accepted computation. With these two boundaries in place it is obvious at once that the Předmost brain has expanded in all of its neopallial areas. The parietal, the occipital and the temporal lobes have all alike assumed greater proportions than in any of the earliest races of mankind. But it is in the frontal lobe that the most remarkable gains are apparent. Not only are the frontal convolutions more prominent and better defined, but that flatness so characteristic of the Neanderthal vertex has disappeared, and there is no sign of that coronal constriction which seemed to characterize the earliest efforts of the cerebrum in the acquisition of its frontal areas.

Metric Evidence of Brain Evolution in Man

The manner in which evolutional progress of the brain has gone forward is readily discerned in the accompanying tabulation. From the Javan man to Homo sapiens there has been a gradual increase in all of the major cerebral diameters. In one particular only has there been the slightest faltering in these increments. The Neanderthal brain shows the greatest transverse diameter. But its superiority in this respect is more than overcome by its marked flatness. A distinguishing metrical feature in the development of the human brain is the consistent gain in length and height from Pithecanthropus erectus to Homo sapiens. The gain in length is to be ascribed largely to frontal increments; that in height is dependent in part upon parietal expansion but also to some extent upon frontal accessions. The bearing of such pronounced frontal evolution upon the ascent of man is evident in the progressive development of human intelligence.

Measurement and Indices of Human Endocranial Casts

Race	Width, [illegible]	Length, [illegible]	Height, [illegible]	[illegible]	[illegible]	[illegible]
Homo sapiens, European average	[illegible]	[illegible]	[illegible]	73		[illegible]
Brünn race					[illegible] 2	[illegible]
Předmost "9"	[illegible]	[illegible]	128	[illegible]		
Předmost "4"	[illegible]	[illegible]	[illegible]	—		
Homo neanderthalensis, La Chapelle aux Saints	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Gibraltar	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
La Quina	132	[illegible]	[illegible]	[illegible]		[illegible]
Homo rhodesiensis	[illegible]	[illegible]		[illegible]		[illegible]
Eoanthropus dawsoni, Piltdown	133	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Pithecanthropus erectus, Java	[illegible]	[illegible]		[illegible]	73 [illegible]	[illegible]

Chapter XXVIII

MAN—PAST, PRESENT AND FUTURE

PREHISTORIC man is gradually emerging from his long obscurity. It is now possible to discern certain attributes of his which still live and are as vital to further human progress as they were to his own day on earth. His skeletal form is known from more than 350 specimens of his fossil remains. These reveal that striking harmony of structure which pervades all human kind. But in them also may be detected many subhuman specializations and numerous variants representing, no doubt, only a small portion of the human experimental types discarded by nature before Homo sapiens was at length derived.

All phases of man's earliest existence are singularly pertinent to modern thought and development. Yet the past has shut in so closely behind us that our racial consciousness is almost wholly restricted to an historical world. This scotomatous view of human existence loses sight of the preparatory biological episodes upon which our being depends.

Evolutional Significance of the Ape-Like Characteristics of Primitive Men

With the appearance of prehistoric man the curtain is lifted to reveal a human perspective of almost impenetrable depth. Looking through this long vista of time it is possible to sense, in some measure at least, the vast distance man has come since his human journeying began. There are milestones along this course which tell of critical turnings and partings of the way. A number of these critical points are indicated by human remains. Certain prominent features of man's skeleton denote that his course did not lead in all directness to the standards of advanced human organization.

Many of his osseous characters were distinctly ape-like—so much so that these appearances in his earliest known state gave him the name of *ape-man*. It may not be denied that pithecanthropus had definite pithecoid resemblances in his skull. The Dawn man of Piltdown manifested similar tendencies less pronounced in the form of his cranium, but still clear in the fang-like character of his canine teeth. The Heidelberg jaw denotes a race in which numerous simian features were still retained, while the men of well-recognized Neanderthal type also bore signs of ape-like specializations in head and face. How otherwise may the massive supraorbital ridge be interpreted, or the broad flat nose, the receding forehead, the widely separated orbits and the large palatal process of the heavy simian jaw?

Nor had Rhodesian man divested himself of these marks of the beast. With the coming of Cro-Magnon times, however, the long experimental period was drawing to its close. Man in near approach to his final modern form had at length arrived. Those many details of simian resemblance were gone. The heavy characters of head and face essential to the contentious life of the great apes had similar reasons for their appearance in the earliest development of man. Judged by the formidable mammals which shared the earth with him, man's life must have been fiercely contested. The offensive equipment of his jaw and head was only feebly supplemented by instrumental devices of his own making. Increasing powers of attack required simultaneous increments of protection. The great apes, gaining in size and strength as compared with the smaller anthropoids had, in this fact, an adequate incentive for the further fortification of their bodies, and especially of their heads. The same incentive was operative in the early differentiations of man, perhaps to an even greater extent. He at least was more venturesome than the anthropoids in risking encounter with the great game animals. Some of his success in these pursuits depended upon cunning, but brute force was not a negligible quality. Innumerable dangerous exposures, mollified in time by adaptive progress and various contrivances, demanded a resistant osseous structure in his cranium to protect his brain. Conditions of his lowly social organization undoubtedly augmented these traumatic contingencies.

FIG. 415. CRO-MAGNON ARTISTS MAKING THE GREAT MAMMOTH FRESCO IN THE CAVE OF FONT-DE-GAUME, DORDOGNE, FRANCE.

Mural painting by Charles R. Knight made under the direction of Prof. Henry Fairfield Osborn. From the Hall of the Age of Man, American Museum of Natural History.

As offensive strength must have been his most effective argument, so a stout frame was his best defense. Is it entirely accurate, therefore, to speak of his bony facial mask, his heavy jaws and large teeth, his thick skull and receding forehead as ape-like specializations? Are they not the more generalized adaptive modifications shared in common by the two branches of the orthograde primate stock, for a life demanding concentrated physical force? Certain specializing factors in these two great lines of primates clearly operate in common. Such, for example, were the marked increase in body weight, the tendency to stand upright, the reduction of speed in escape, the progressive loss of arboreal retreat, the need of augmented offensive powers and a more capable mechanism for procuring food supply. All of these appear as vital necessities in the specialization of man and the great apes. If certain structural features determined by these physiological demands became progressively less prominent in man, it was because his genius gradually devised the means to obviate their need. In fact, it was the potential degree of cerebral growth and psychic development which kept the human cranium so plastic.

It is questionable, therefore, whether any advantage is gained by the continued reference to the pithecoid specializations of primitive man. If he were ape-like in many aspects of his form and being, the great apes to offset this have been called man-like on similar grounds. This convenient interchange in terms does no doubt signify a mutuality in definite characteristics. On the other hand, it tends to obscure the common generic factors which imparted to man and ape alike those distinctive characters described in the human as pithecoid.

The Five Essential Hominid Characters

That there was a definite prehuman stock, a stock capable of producing both anthropoid apes and man, cannot be disputed. But at least five critical and closely interdependent specializations determine the status of the human race: the appearance (1) of the human brain, (2) of the human foot, (3) of the human hand, (4) of the erect posture with bipedal locomotion, and (5) a terrestrial mode of life.

Estimated by these hominid characters, the human type was irrevocably established despite such pithecoid features as it might still retain. When this status of man is reached, however low and humble it may be, there is little justification for the term ape-man. By the fact of his entrance into the human family, man surpassed the more narrow limitations of simian organization. At the same time he retained within himself a structural plasticity for further development which the apes had almost entirely sacrificed to their definitive specialization.

Some Views of Man's Relation to the Apes

The human race in this sense bears no ancestral relation to any of the known apes, either living or extinct. Man is distinguished because he was able to establish his own family in the animal kingdom by separating himself from the formal restrictions which bound the apes to their simian habitat and structure. In a recent communication, Professor Osborn (*Natural History*, xxvi, No. 3, p. 269) has taken a position in decisive terms which gives the human race a line of ancestors entirely its own and quite distinct from that of the anthropoid apes. "Man and all his ancestors," he writes, "should now be embraced within the family hominidae as distinguished from the family simiidae which embraces all of the anthropoid apes. This family distinction naturally carries with it the appellation 'Dawn Man' as distinguished from the appellation 'Ape-man' which will gradually disappear through disuse along with other misleading terms, due to our misconception and ignorance as to the actual ancestors of man."

Over against this view, it is only fair to quote the opinion of two other eminent authorities, Professor Gregory and Professor McGregor. Both take exception to this interpretation on the ground that it may be misleading. They are generally agreed that the earliest known races of mankind were already true hominidae and, therefore, in spite of certain ape-like features, they hardly deserve the name of "ape-men." They are unwilling, however, to disclaim all kinship whatsoever of the human race with the anthropoid apes. Such kinship does not imply a direct ancestral relation but indicates an evolutional process among the primates which places the chimpanzee and gorilla closer to man than to any tailed monkey.

In one respect the brain lends unquestionable support to Professor Osborn's view. In the lowest known type of man, Pithecanthropus erectus, cerebral development had attained human proportions. The critical expansions in the frontal, the parietal and the temporal lobes are decisively man-like. They seem sufficient to raise the Javan man out of the class of ape-men, even if such a class should eventually maintain its validity. Furthermore, the human brain from its most humble beginning, has, unlike the brain of the great apes, manifested advances in specialization of those areas associated with the production of spoken language, with the regulation of highly skilled acts and, most probably at least, with unidexterity.

Progressive Development as the Outstanding Feature of the Human Brain

Thus from its inception the cerebrum endowed man with the capacity to develop, inculcate and transmit certain cultural activities. With the first rude fashioning of implements from wood or bone, there arose that uninterrupted stream of human achievement which has passed on as the main current of all culture and knowledge. It was this power of progressive and racial learning that made the human brain distinctive as compared with all others. Conditioned reflexes of the first, second and third order develop in many other mammals, but man soon transcended this limited conditional range. His eventual successes came from his almost unrestricted capacity to utilize the conditions imposed by his own experience or imparted to him by the didactic efforts of others. The kind of brain he possessed is not only apparent from the structure of this organ, but quite as much from his mode of life and handicraft. Viewed in the light of his many cultural phases, man's outstanding attribute has been his power to improve. From age to age, from race to race, he has shown a steady progress in the control of material conditions as well as in the development of spiritual understanding. Allowing for the not infrequent cultural fluctuations during which human attainments have waned while the higher human qualities were conspicuous by their absence, man's tendency as a race under favorable conditions has been to advance.

Cultural Periods as Evidence of Cerebral Development. It is probable that he had an actual *Eolithic period* when the stone implements he produced had all the crudity of accidental forms. The many adaptive im-

FIG. 416. NEOLITHIC MEN.

These men lived along the shores of the Baltic in the early stages of the New Stone Age. They were the direct forerunners of civilization. They cultivated the soil, domesticated animals, made pottery and woven textiles, erected sepulchres and temples of stone (dolmens and megaliths). Painted by Charles R. Knight under the direction of Prof. Henry Fairfield Osborn. From The Hall of the Age of Man, American Museum of Natural History.

provements in his flints during the pre-Chellean, Chellean and Acheulean periods, led by progressive stages to his pronounced Mousterian productiveness. More striking still was his Aurignacian development with its remarkable outburst of esthetic enthusiasm and artistic creations. If after the Solutrean era his industries began to languish, actually sinking to a low level in the Azilian period, it seems only in preparation for the advent of Neolithic man.

The Cro-Magnon decadence may well have cleared the way for a transition which was to prove portentous in its material and psychic advance. It ushered in a period of practical utilities. It substituted the benefits of applied science for the delusions of expedient sorcery. Neolithic man may have prayed for his crops, but he also tilled the soil and planted seed. He may have had propitiatory ceremonies for his hunting expeditions, but he domesticated animals to guarantee an assured supply of food. The efficiency of reproducing the likeness of game animals in dark caverns no longer appealed to his common sense. Unlike his Neolithic successor, the Cro-Magnon was satisfied, according to his lights, by the delusions of his hunting magic and art sorcery. But Neolithic man had discovered the magic of agriculture and sought to control nature by the toil of his hands rather than by impractical incantations. As farmer and herdsman he naturally became a landholder. This was a long and provocative step in the direction of modern humanity. It enforced upon man the need to defend his claim and assert his right. Quickly enough this new assertiveness led to the more aggressive Ages of Bronze and Iron with their harsher organizations for offense and defense. Ultimately it extended its influences into historical times, creating all of the armed camps known as civilization, ancient, medieval and modern.

Mankind's Future Paths of Progress

The Hominidae have been a truly progressive family, by reason of which it differs from all others in the animal kingdom. Here and there about the world it has lagged in its advances. But given its fair opportunity, it has not failed to go forward. The line of this progress may not be deemed wholly satisfactory by the standards of enlightened criticism. Yet in bending the forces of nature more and more to his will and convenience, man has surely progressed. Where he has stood still, perhaps even fallen behind, is in the manifest lack of control over his own nature.

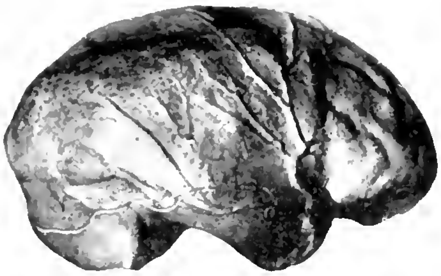
Professor Pavlov, in his epoch-making work on the Conditioned Reflexes, has vividly portrayed this situation, voicing at the same time the hope of a possible escape from it. While the pall of revolution still hung over him in Soviet Russia, he wrote these inspiring words:

"I am deeply and irrevocably convinced that here along this path leads the way to the final triumph of the human mind over its utmost and supreme problem—the knowledge of the mechanism and laws of human nature. Only hence may come a full, true and permanent human happiness. Let the mind rise from victory to victory over surrounding nature; let it conquer for human life and activity, not only all the surface of the earth, but the water and surrounding atmosphere; let it transfer for its purpose prodigious energy from one part of the earth to the other; let it annihilate space for the transference of its thoughts—yet the same human and his mind leading him into dark powers, to wars and revolutions, with their horrors, not calculating the material loss and inexpressible pain, reproduces animal relations. Only science—the exact science about this same human and the most sincere approach to it from the side of Omnipotent Nature will deliver man from his present gloom and will purge him of his contemporary shame in the sphere of human relations."

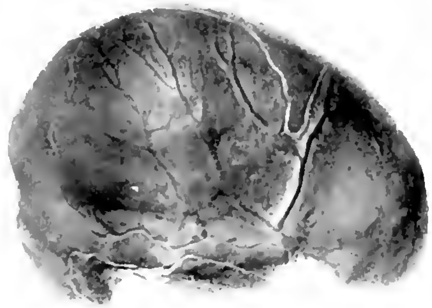
The brain of prehistoric man seems to shed new light upon this path. It seems to give assurance of that deliverance which Pavlov confidently believes awaits mankind.

THE FRONTAL LOBE—ITS POTENTIALITIES FOR HUMAN PROGRESS IN THE FUTURE

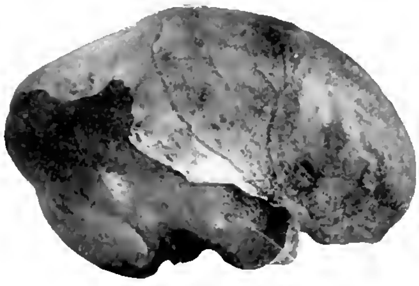
Since his earliest beginning man has grown in humanity as his brain expanded. Such a conclusion appears irresistible. A comparison of the cerebrum in the stages of human evolution already known to us is sufficient to convince the most skeptical. Placed side by side (Figs. 417–422), brain casts of the Javan and the Piltdown man, the Rhodesian and the Neanderthal, the Predmost and the modern, demonstrate more effectually than words the extent of this progress. The regions in which expansion has been most pronounced are easily discerned. Increments in the parietal and temporal areas



Pithecanthropus



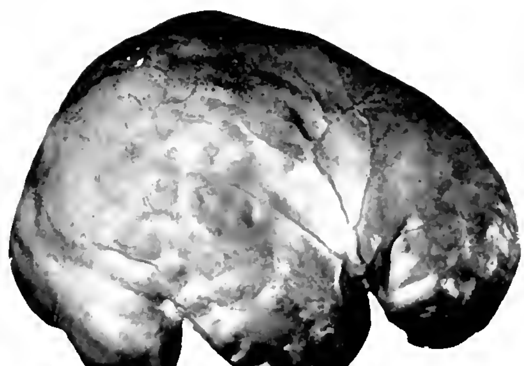
Piltdown



Rhodesian

Neanderthal

Predmost



Modern

FIGS. 417 TO 422. A COMPARISON OF THE ENDOCRANIAL CASTS OF PITHECANTHROPUS, PILTDOWN, RHODESIAN, NEANDERTHAL (LA CHAPELLE AUX SAINTS) AND PREDMOST MAN WITH HOMO SAPIENS (MODERN TYPE).

have been steadily maintained throughout this series, but it is in the frontal lobe that decisive advance has occurred. This area, so poorly represented in man's nearest kin, the great anthropoid apes, shows exuberant growth in pithecanthropus. Its features correspond with those of Homo sapiens in nearly all details. Its only essential inferiority is its relative smallness. Yet even its size is sufficient to justify admission into the human family. Its specializations in the prefrontal area, and the development of the inferior frontal convolution denote the acquisition of human speech and reason.

Perhaps it is hazardous to define any single area in the brain as the region supreme in cerebral organization, since the entire neopallium is virtually interdependent throughout all of its special parts. The visual, the auditory and the somesthetic sensory areas contribute so indispensably to life's reactions, that one part may not be subordinated to another. This is also true of the motor area, the area regulating skilled movement and the large intermediate zone which partakes of parietal, occipital and temporal characters. Each of these areas has progressively expanded through the several evolutional stages of the human brain. Yet it is reasonable to attribute a certain superiority to that neopallial region which is charged with the functional representation of all other cortical territories, which combines the highly particularized functions of all other areas in broader impressions of human existence, which acts as the accumulator of experience, the director of behavior, and the instigator of progress. Traced through all their intermediate steps upward it is exactly these prefrontal and frontal regions which manifest the most conspicuous development. The process of this long continued progressive expansion in the frontal lobe, reaching back to the earliest Pleistocene times, and it may be even into the Pliocene epoch, conveys the impression of a responsive plasticity in the human brain. This remarkable antiquity and this salutary plasticity have been largely overlooked. For the most part the human cerebrum is regarded as a finished product. Its evolutionary history does not support this point of view, but makes it appear far more probable that the brain of modern man represents some intermediate stage in the ultimate development of the master organ of life. And the greatest possibility for future progress lies in the further development of the frontal lobe. In this sense the brain of prehistoric man is of more than antiquarian interest. It has a positive bearing on the future advances of mankind.

PART V

EVOLUTIONAL MODIFICATIONS OF THE PRIMATE CEREBRUM CULMINATING IN THE HUMAN BRAIN

INTRODUCTION TO PART V

THE aim of these concluding chapters is to consider certain questions whose discussion may seem to justify the deductions drawn from the facts as they have been presented.

The questions are primarily designed to give the evidence its final logical arrangement, to test, in so far as may be possible, its validity. They have been formulated as follows:

1. Does the appearance of the brain in primates, including the lemurs, monkeys, apes and man, show such similarity of structure as to indicate a constancy which distinguishes them as a distinct and separate order of mammals? And does this homogeneity receive substantial proof in the essential similarities of behavior within this order?

2. Do the structural patterns of the brain in these primates manifest progressive modifications in harmony with progressive adaptations in the behavior of these animals?

3. Do these progressive modifications in structure and behavior justify the conception of an evolutional process in consequence of which fundamentally simple structures have become more complex in order that they might impart to behavioral reactions an increasing range of adaptability?

4. Does the primate brain indicate that man was derived from a series of preparatory pro-human stages and what relationship does it reveal between man and the apes?

The Position of the Primates among the Mammals

In considering these questions it is first necessary to assign the primates to their proper position among the mammals. They are but one of many contemporaneous mammalian orders. If, as is generally believed, a period of time reaching back to the inception of the Tertiary period was required to complete the adaptive modifications of the primates, they were by no means the only forms undergoing an active process of differentiation. From some period in the Mesozoic a host of primitive mammals began to pass into the great habitat zones along many different lines of adaptive radiation. This process of mammalian differentiation led up to the era of geological time properly called the age of mammals, more particularly, perhaps, the age of placental mammals. Even at the beginning of the Tertiary period there had appeared such diversified forms as the carnivores (creodonts), bats, insectivores, hoofed mammals (protoungulates), rodents, lemuroids and tupaioids. All of these orders developed a profusion of families, genera and species, linked together, however, by one mutual bond of heritage in their placental mode of development. The duration of this great division of time is variously estimated between ten million[1] and one hundred and forty million years.[2]

[1] American Museum of Natural History estimate.
[2] By radium emanation method.

CHAPTER XXIX.

THE SIGNIFICANCE OF THE STRUCTURAL HOMOGENEITY AND SPECIFIC MODIFICATIONS IN THE PRIMATE BRAIN. THEIR RELATION TO THE PROGRESSIVE ADAPTATION OF BEHAVIOR

THE ...

exceed a forebrain index of 60 per cent. In the main they are all much below this figure. The forebrain indices in the dogfish, codfish and shark are all less than 25 per cent of the total brain volume. A reptilian form, such as the soft-shelled turtle, shows the considerable advance to 53 per cent, while the American ostrich with 60 per cent reaches the high level of develop-

Encephalic Indices of Evolutional Significance

Animal	Volume index: Forebrain per cent	Volume index: Midbrain per cent	Volume index: Hindbrain per cent	Weight index: Forebrain per cent	Weight index: Midbrain per cent	Weight index: Hindbrain per cent
Index: 82 and above			Hands Fingers Finger nails			
Homo sapiens, modern man	88	1	11	87	1	12
Troglodytes gorilla, gorilla......	84	2	14	84	2	14
Simia satyrus, orang-outang .	83	5	12	83	5	12
Macacus rhesus, Indian monkey	83	2	15	84	2	14
Hylobates hoolock, gibbon	82	2	16	82	2	16
Callithrix jacchus, marmoset.	83	2	15	83	2	15
Index: 70 to 80			Paws Hoofs Claws			
Canis familiaris, dog	80	7	13	80	5	15
Felis domestica, cat ...	77	6	17	75	4	21
Equus caballus, horse ...	80	2	18	80	2	18
Bos taurus, cattle .	80	2	18	80	2	18
Camelus bachtr., camel	79	2	19	79	2	19
Elephas indicus, elephant	72	2	26	71	2	27
Myrmecophaga jub., giant ant-eater....	75	6	19	73	5	22
Bradypus tridact., three-toed sloth.	70	10	20	70	10	20
Index: 20 to 60			Wings Fins Paddles			
Rhea americana, ostrich	58	16	26	60	13	27
Aspidonectes ferox, soft-shelled turtle	57	15	28	53	20	27
Rana sylvatica, frog				21	37	42
Gadus morrhua, cod-fish .	20	40	40	20	40	40
Squalus acanthias, dog-fish				23	27	50

ment in this type of vertebrate. Animals developing claws, hoofs and paws in the forelimb differentiation have a forebrain index which may rise to, but does not exceed 80 per cent. For the most part it is much below this figure. The sloth, the anteater and even the elephant all have a value below 76 per cent. The camel, the horse and the dog reach the upper limit of 79 or 80 per cent which seems characteristic of animals whose forelimbs are conditioned by development as specified. In that group in which manual differentiation reaches its final stages, the hand presenting fingers and fingernails, the forebrain index is always above 80 per cent. It ranges throughout the primates from 81 per cent in lemur to approximately 90 per cent in man. The significance of these comparative indices takes its importance from the fact that the forebrain is the most recent accession to the central nervous system and attains its greatest expression in mammalian orders, particularly in the primates. It is the structure essential to the most highly organized behavioral regulation. Animals possessed of the greatest development in this respect manifest the greatest adaptability in meeting the conditions of their environment. They are better able to adjust themselves and enjoy a greater range of activity. The primates stand in contrast to all other vertebrates because they possess the most effective organ for the utilization of their environmental opportunities.

The Diametric Indices of the Primate Brain. The diametric indices of the brain establish an ordinal character which also distinguishes the primates among mammals. In these animals the ratio of the interparietal diameter to the occipito-frontal diameter varies from .81 to .88. Compared with carnivores, ungulates and marsupials, the contrast is striking. It indicates the type of brain whose longitudinal expansion is concomitantly followed by a transverse expansion. In other words, the brain is becoming broad and losing some of that elongated appearance which is characteristic of lower mammalian forms. This condition of *broad brainedness*, if such it may be termed, is a characteristic of the primates. In effect it is the consequence of expansion taking place in the neopallium which begins to overshadow the archipallium (rhinenecephalon). The chief increments are at first evident in the parietal lobe, indicating no doubt the expansions in somesthetic sensibility due to quadrumanal differentiation. Corresponding expansion soon makes itself apparent in the temporal and occipital lobes. It finally expresses itself, at the upper extremity of the primate series, in large increments to the frontal lobe. This dimensional modification is expressive of a recession in the rhinenecephalon, particularly involving the olfactory sense which is gradually replaced in the primate by an extensive development in the distance receptors for sight and hearing. In certain other groups of mammals there is a marked degree of broad brainedness, for example, that seen in seals, cetaceans or sirenians. In these instances the brains are almost as broad as they are long, and thus transcend the upper limit already prescribed by the diametric indices of the primate brain. In the case of aquatic mammals, the underlying motive in the transverse expansion of the hemispheres is different from that in the primates. It particularly affects the parietal area in relation to expanding the region of somesthetic sensibility. These animals, by their entire body surface, are in constant contact with the water. Their somatic sensory surface thus becomes a most important receptor system and because of its great extensiveness determines the corresponding expansion of the parietal lobe. Some of the aquatic mammals also show a recession in the prominence of the rhinenecephalon and the olfactory sense, which may even exceed that witnessed in apes and man. They show, however, no such expansion in the frontal or occipital regions as that seen in the primates.

The Fissural Pattern of the Hemispheres in the Primate Brain. The fissural pattern of the hemispheres is identical with or follows a design similar to the human adult. The convexity of the cerebral hemispheres has in general a tri-fissural design in which three chief fissures are present: first, the fissure of Sylvius, second, the fissure of Rolando and third, the simian fissure. The position and angulation of these fissures are characteristic in the primate brain. The Sylvian fissure in its lateral portion extends backward and upward at an angle something less than 45 degrees with the base line of the brain. The fissure of Rolando extends forward from the superior longitudinal fissure at an angle varying from 67.5 to 84 degrees. The sulcus simiarum leaves the superior longitudinal fissure at an angle of about 90 degrees. This latter sulcus is believed to have no counterpart in the human brain. Nevertheless, distinguished authorities such as Elliot Smith maintain that the sulcus lunatus, on the lateral surface of the occipital lobe of man, is a vestige of this great simian fissure. In many instances the human parietal incisure of the occipito-parietal fissure corresponds in striking degree to the more proximal portion of the sulcus simiarum of the higher anthropoids.

Nor are the similarities, which link the primates together on the basis of their fissural patterns, limited to these three major fissures alone. With few exceptions, the identifications may be carried to the secondary fissures. In many lower primates and also in the intermediate group, these secondary fissures have no such prominence as they attain in man. If the brains of such simians be compared with the fetal brain of man in which the secondary fissures are making their appearance, the correspondence between the anthropoid and human brain may be recognized. Further development of the brain in man adds much complexity both to its convolutions and fissures. But an essential correspondence of fissural pattern exists in all primates.

THE LOBATION OF THE PRIMATE BRAIN. The lobation in apes and man is identical throughout the series. As seen upon the lateral convexity of the hemispheres, this lobation expresses itself in four distinct divisions: the frontal lobe, the parietal lobe, the temporal lobe and the occipital lobe.

FIGS. 423 AND 424. SIZE AND CONFIGURATION OF THE DORSAL SURFACE OF THE HUMAN BRAIN COMPARED WITH THAT OF LEMUR MONGOZ.

FIGS. 425 AND 426. SIZE AND CONFIGURATION OF THE LATERAL SURFACE OF THE HUMAN BRAIN COMPARED WITH THAT OF LEMUR MONGOZ.

This lobation corresponds so much in detail throughout the order that there can be no doubt as to the essential similarity existing in these morphological features of the central nervous system.

THE CONVOLUTIONAL PATTERN OF THE PRIMATE BRAIN. This pattern coincides with striking consistency. Wherever convolutions develop, their general homologies may be easily determined, if not by actual comparison with the adult human brain, at least with some earlier fetal stages.

ORBITAL AND OCCIPITAL CONCAVITIES OF THE PRIMATE BRAIN. The two great concavities on the basal surface of the brain, known respectively as the orbital and the occipital concavity, may be identified as corresponding features in all species.

CERTAIN CHARACTERISTICS OF THE BASAL SURFACE. Certain basal characteristics are notably similar. Thus the olfactory bulb and its associated structures have become much reduced in size as compared with the carnivores and ungulates. This is especially the case with the olfactory tracts which are readily detachable from the under surface of the brain as far back as the trigonum olfactorium. In no instance does either the tract or the bulb contain that prolongation of the ventricular cavity common in lower mammals. Another characteristic on the basal surface is the relation of the optic nerves and optic tracts to the chiasm in primates. The optic nerves approach the chiasm and the tracts leave it at an angle much nearer 90 degrees than it is in any lower mammalian forms. When retracted the olfactory bulb and tract usually reveal the beginning of a small sulcus immediately in front of the trigonum olfactorium. This is the sulcus olfactorius which more or less completely bounds a gyre situated mesial to it, the gyrus rectus. The sulcus olfactorius and the gyrus rectus occur in an incipient stage or fully developed in all of the primates.

RELATION OF THE CEREBELLAR HEMISPHERES IN THE PRIMATE BRAIN. The relation of the cerebellum to the cerebral hemisphere is another identifying characteristic in the primate brain. In all species, with the exception of the lemur, often mentioned as a transitional form, the occipital lobe of the hemisphere has so advanced in its development as entirely to conceal the tentorial surface of the cerebellum. Not alone in the relation of the cerebellar to the cerebral hemispheres are the primates distinguished from all other mammals. There appears another identifying feature on the occipital surface of the cerebellum, i.e. the vallecula, or vermal notch, which is most characteristic of the order. The depression between the two lateral cerebellar lobes, which lodges the inferior vermis, is also a distinctive mark. The ventral surface of the brain likewise reveals prominent indices connected with the development of neokinetic functions, such as the pyramid, the inferior olivary body, the pons Varolii and the cerebral peduncles.

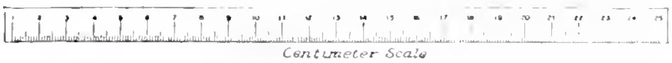
THE DEVELOPMENT OF THE PINEAL FOSSA IN THE PRIMATE BRAIN. The development of the pineal fossa lying at the cephalic extremity of the intercollicular sulcus makes provision for the epiphysis cerebri. The relation of this gland to the midbrain is subject to considerable variation among mammals. In some it occupies a supracallosal position. In other forms it is postcallosal, lying behind the splenium of the corpus callosum but not in contact with the midbrain. In the primates, it lies in a subcallosal position, resting upon the roofplate in the pineal fossa of the midbrain.

Such are the features on the external surface of the brain which constitute an array of similarities sufficient to establish the ordinal solidarity of the primates. Each of these distinctive features may not in all instances have the indubitable quality of an identifying character. But the sum total of them all serves as an entirely reliable guide for the identification of any member of the primate group.

INDICATIONS OF EVOLUTIONAL DEVELOPMENT IN THE PRIMATE BRAIN

In connection with such distinctive features the question naturally arises whether these characters are subject to such modifications as show

FIGS. 427 AND 428. SIZE AND CONFIGURATION OF THE DORSAL SURFACE OF THE HUMAN BRAIN COMPARED WITH THAT OF CALLITHRIX JACCHUS, THE MARMOSET.



FIGS. 429 AND 430. SIZE AND CONFIGURATION OF THE LATERAL SURFACE OF THE HUMAN BRAIN COMPARED WITH THAT OF CALLITHRIX JACCHUS, THE MARMOSET.

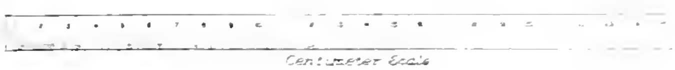
a progressive evolutional development. In other words, does each one of these features have its simplest morphological expression in the lowest of the primates, and pass progressively through graded intermediate stages, to a culmination of its greatest complexity in the highest member of the order?

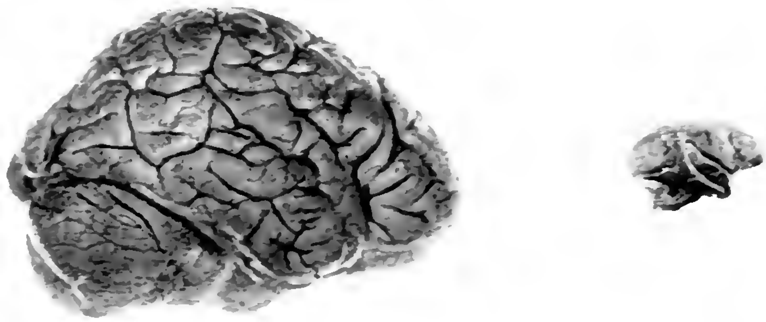
Evolutional Significance of Brain Indices. In the matter of the brain indices it is certain that the primates show a steady and progressive advance. There are some incidental fluctuations, however, which may be attributed to variations in the degree of specialization. Thus the lemur, the tarsier and the marmoset stand at the lower end of the series in so far as the forebrain index is concerned, each of these genera being slightly above 80 per cent in this respect. The intermediate group is next in position. The great anthropoids, although they show a definite increase in their forebrain index, are still considerably below man. The accompanying tabulation indicates the tendency toward expansion as witnessed by this index among the primates.

Encephalic Indices

Animal	Encephalic index (per cent)		
	Forebrain	Midbrain	Hindbrain
Lemur	81	5	14
Marmoset	80.5	9.5	10
Mycetes	81.6	4.8	13.6
Baboon	83	3	14
Macacus	84	2	14
Gibbon	81	5	10
Orang-Outang	83	5	12
Chimpanzee	83	5	12
Gorilla	84	1	14
Human	86–89	1	10–13

FIGS. 431 AND 432. SIZE AND CONFIGURATION OF THE DORSAL SURFACE OF THE HUMAN BRAIN COMPARED WITH THAT OF MYCETES SENICULUS, THE RED HOWLING MONKEY.





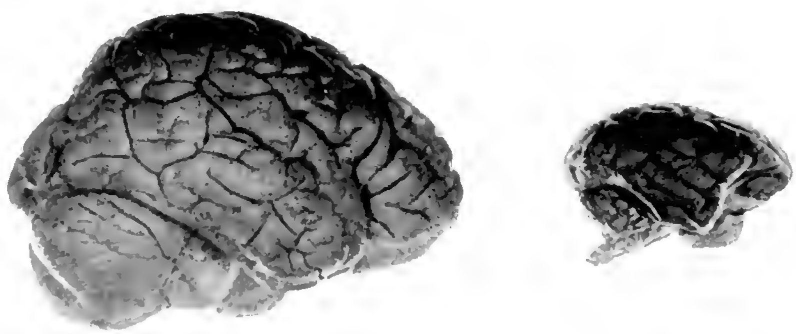
FIGS. 433 AND 434. SIZE AND CONFIGURATION OF THE LATERAL SURFACE OF THE HUMAN BRAIN COMPARED WITH THAT OF MYCETES SENICULUS, THE RED HOWLING MONKEY.

Evolutional Significance of Cerebral Fissures. In the matter of fissural pattern, the primate brain presents few difficulties in analysis. As might be expected of a transitional form, the lemur does not disclose a pattern entirely harmonious with the primate formula. The fissures in lemur have shown a considerable specialization of their own. Far from being a lissencephalic hemisphere awaiting, as it were, the impress of adaptive influences, the lemur brain manifests a distinctive effort in its gyrencephalic specialization. Its fissural pattern is, to a degree at least, reminiscent of a carnivore type of brain. In it may be seen some of that tendency, peculiar to fissures in carnivores, to arrange themselves in circumsylvian arches. But even if the brain of lemur is slightly suggestive of this arcade-like arrangement, it has broken away from older influences in this direction and established certain designs of its own. The anterior and posterior rhinal fissures, characteristic of the carnivores in general, have now disappeared from the lateral convexity due to the marked extensions in the temporal lobe. The lemur thus indicates in its temporal region a distinct advance over any possible subprimate prototype, and the Eocene predecessor of the lemurs (Adapis) had a brain even less developed. The fissure of Sylvius in lemur begins to assume the more oblique relations notable in the primates. The sulcus intraparietalis is well defined, as is also the sulcus parallelus (superior temporal). The beginnings of a central sulcus of Rolando may be discerned on the boundary between the frontal and the parietal lobes. What the lemur brain lacks, however, is any extensive occipital specialization upon the convexity of the hemisphere.

The phyletic history of the Sylvian fissure contributes convincing evidence regarding the evolutional significance of the fissural pattern of the brain. As interpreted by Elliot Smith (1903), who doubtless has given this subject the most extensive and authoritative consideration, the fissure of Sylvius is a composite whose elements vary considerably in different mammals. The most constant of these components is the supra-Sylvian fissure. The mammalian sulcus usually homologized with the fissure of Sylvius in apes and man is, according to Elliot Smith, nowise homologous. He calls this subprimate indentation, when it occurs, the *pseudo-Sylvian sulcus*. This sulcus may be absent, as in Viverra and Hyrax, or its composition may include different elements in different orders. Thus the pseudo-Sylvian sulcus of the carnivores may differ from that of the ungulates, in which latter the fissure often results from the fusion of two infoldings analogous to the ecto-Sylvian sulci of the carnivores. Concerning these latter fissures, there can be little doubt but that they are morphologically unimportant, and appear for the most part as furrows compensatory to the invagination of the pseudo-Sylvian fissure. In Smith's fissural pattern of the hypothetical generalized carnivore this pseudo-Sylvian element does not appear. The mammalian generalized pattern includes the supra-Sylvian, the orbital (pre-Sylvian), coronal, lateral, post-Sylvian and cruciate sulci.

The Sylvian fissure in lemurs is formed by the merging of the pseudo-Sylvian and supra-Sylvian sulci. In this complex the supra-Sylvian element is the most constant in all lemurs, just as it is in most mammals. Generally speaking, this stable and constant sulcus by its union with the variable suprarhinal indentation called the pseudo-Sylvian sulcus gives an ultimate fixity to the latter. The result of this fixation is the posterior limb of the fissure of Sylvius. In monkeys and apes the only portion of the fissure which develops is this posterior limb. The fully formed anterior limbs are never found except in man. Thus the Sylvian fissure in its complete form occurs only in the human brain where it exists as a combination of the supra-Sylvian (superior limiting) sulcus, the pseudo-Sylvian (inferior limiting) sulcus, and the diagonal (anterior limiting) sulcus. Viewed in this light the formation of the fissure of Sylvius may be understood to represent a consistent evolutional process throughout all gyrencephalic mammals.

FIGS. 435 AND 436. SIZE AND CONFIGURATION OF THE DORSAL SURFACE OF THE HUMAN BRAIN COMPARED WITH THAT OF PAPIO CYNOCEPHALUS, THE BABOON.



FIGS. 437 AND 438. SIZE AND CONFIGURATION OF THE LATERAL SURFACE OF THE HUMAN BRAIN COMPARED WITH THAT OF PAPIO CYNOCEPHALUS, THE BABOON.

In most of the lemurs the post-Sylvian sulcus is a simple linear furrow representing the parallel or superior temporal sulcus in apes and man.

With reference to the central (Rolandic) fissure in lemurs, there is some difference of opinion. The slight indentation between the frontal and parietal areas has been called by Jacobsohn and Flatau the precentral sulcus, a view which disregards the fact that such a sulcus never occurs in the absence of the more stable central fissure. The tendency in all lemuroids is toward a fusion of this frontal indentation with the caudal extremity of the coronal sulcus which produces that great transverse fissure, the central (Rolandic) sulcus of apes and man.

The fissural pattern of tarsius is simple in the extreme, presenting as it does but a single indentation, the fissure of Sylvius. This is undoubtedly the suprarhinal fold corresponding to the mammalian pseudo-Sylvian sulcus. In this sense the neopallium of tarsius is the most generalized of all the lower primates. It thus stands closest to some subprimate lissencephalic brain which was the forerunner of the simian cerebrum. Tarsius at the same time is more pithecoid than the lemurs in the development of its visual cortex and in the appearance of a posterior cornu in its lateral ventricle. With this combination of generalized characters and pithecoid tendencies, the brain of tarsius serves particularly well as the transition stage which carried upward from some insectivore-like type the basic characters of mammalian cerebral organization but also felt the decided impetus toward simian development. It has remained dynamically more plastic than the brain of lemurs, which latter (however primate in their proclivities) have experienced a specialization quite their own, due, it may be, to secondary retrogressive modifications.

If, as first suggested by Huxley and subsequently insisted upon with added emphasis by Osborn, the ancestral type of placental mammal was an animal resembling the tree shrew (Tupaia), then it is probable that the differentiation which led to the various orders of mammals started from some simple lissencephalic condition, showing only the most primitive fissures. It may, therefore, be concluded that the fissural prototype of the primate order is already laid down in the lemur brain. Such departures as it makes from the ultimate design may be ascribed to specific specializations in the lemurs themselves. To whatever extent they experienced the primordial incentive toward primate differentiation, there was that in their organization which determined characteristics strictly *sui generis*, yet imparted to their specialization such tendencies as amply justify their inclusion in a separate suborder of the primates.

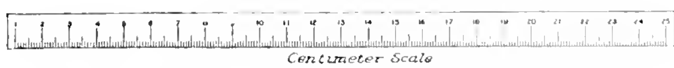
The brain of the marmoset, on the other hand, which declares itself in so many features as inherently primate, affords that more generalized pattern in its fissural arrangement from which all of the families in the anthropoidea could take their beginning. The brain of Callithrix jacchus might easily be descendant from some primitive lissencephalic type. It presents but a single well-defined sulcus, the fissure of Sylvius, with the faintest inception of a superior temporal sulcus. Except for these landmarks, the lateral surface of the hemisphere is quite without sign of fissural inscription. With this as yet unprejudiced surface of the neopallium, influenced alone by the correct position of its Sylvian fissure, the marmoset brain appears to be waiting for the further impress of those fissural markings characteristic of the more advanced primates. This relatively simple condition of the neopallium in Hapalidae is in harmony with what has already been observed in reference to their simple behavioral characters. The departure of this family from the primitive primate stock was doubtless a retrogressive one, less significant in what it produced of itself than in its prophetic indications of actual simian tribes to come. In the lemur brain and in the brain of marmoset two contrasting tendencies in the early primate differentiation are represented. In the first instance the lemur, representing the incipient primate impulses, furnishes evidence of response along these lines and at the same time yields to influences of specialization which divert it into a path of its own. In the case of the marmoset, the impulse toward anthropoid evolution is more strongly active as a generalized influence, not yet specific enough to determine those indelible cerebral characters which are sufficient to distinguish all of the other families, genera and species in the suborder anthrepoidea. That the full force of the tendency toward simian differentiation is ultimately felt by all of the monkeys of the new world is clearly attested by the fissural patterns of these primates. The Cebidae reveal what was definitely attempted in the differentiation of the lemur's brain, subject perhaps to some frustration by other influences, but again somewhat feebly aimed at in the marmoset's brain. All of the new world simians present a fissural pattern which marks them as members of the suborder anthropoidea. The Sylvian fissure takes a more oblique course backward and upward, separating the parietal from the temporal lobe.

The central sulcus, which represents the fissure of Rolando, is now well defined and forms the boundary between the frontal and parietal lobes. The sulcus parallelus (superior temporal fissure) is distinct, as are also the intermediate temporal and the intraparietal fissures. The greatest degree of fissural specialization occurs in the temporal and parietal lobes. Only the slightest indication of fissures is found in the frontal and occipital regions of the brain. In fact, neither of these lobes shows any marked extent of expansive development, thus no doubt accounting for the high degree of broad brainedness recorded in Mycetes seniculus. In the frontal region there is a slight indenture indicating the superior frontal sulcus, and one somewhat more pronounced marking the position of the inferior frontal sulcus. In the occipital lobe, which is but slightly developed, there is a faint indication of that remarkable sulcus which identifies all of the simian tribe, the sulcus simiarum. This fissure appears in mycetes as well as in other Cebidae as a small transverse groove, identified by Elliot Smith and others as the sulcus occipitalis transversus, which Retzius maintains is the homologue of the sulcus simiarum ("Affenspalte"). Lateral to this transverse occipital fissure is an equally faint groove indicating the position of the sulcus occipitalis lateralis. With reference to the sulcus centralis, or fissure of Rolando, it may be said that in the brain of the Cebidae, particularly in the brain of mycetes, this fissure has much that is reminiscent of the fissura cruciata of the lower mammals. There is, however, an important difference. Its angle of inclination with reference to the superior longitudinal fissure is now considerably less than 90 degrees. In mycetes, therefore, as in most of the new-world monkeys, the fissural fundaments of the primate brain are clearly discernible. Hereafter, in the further steps of evolutional development, it is simply a matter of increasing complexity, particularly of expansion in the frontal and occipital lobes, which brings into existence all of the fissural characters of the highest primates.

In the lower division of the old-world monkeys, here described as the intermediate primates, the simian characters in the fissural pattern of the brain appear in their ultimate prominence. The pattern is now definitely trifissural with a fissure of Sylvius, a fissure of Rolando and a simian fissure constituting easily recognized boundary lines between the four great lobes appearing on the lateral convexity of the hemisphere. The fissure of Sylvius has departed from its primitive vertical direction and is tending to approach closer to the horizontal, characteristic of it in the higher species. The fissure of Rolando also has reduced the angle of its inclination in reference to the superior longitudinal fissure and now runs a course of something over 75 degrees with the median plane. The sulcus simiarum extends outward from the superior longitudinal fissure at an angle of 90 degrees and reaches as far lateral as the lateral occipital fissure. In the baboon, Macacus rhesus and in the gibbon, these fissural relations are all essentially similar. In none of the three species does the fissure of Rolando show more than a suggestion of its two major genuflections. In all of the three the most prominent and deep fissuring is seen in the parieto-temporal area; in the frontal area only the beginnings of the superior frontal fissure are apparent. The precentral fissure is well defined, while in the occipital lobe two fissures are clearly marked. These are the fissura occipitalis and the lateral occipital fissure. All semblance of the typical circumsylvian arrangement of the sulci has now disappeared. In the great anthropoids the fissural pattern has increased considerably in its complexity, although it retains all of the fundaments which have been traced through the serial approach to this level of the primate order. The lateral convexity is still trifissural, the fissure of Sylvius, the fissure of Rolando and the simian fissure constituting the main landmarks.

As in all the intermediate group, notable expansions are seen in the occipital and frontal lobes; indeed, it is in these regions that the greatest degree of complexity has made itself apparent in the arrangement of the fissures. The central sulcus of Rolando now manifests a definite tendency to display its major genuflections so characteristic of the human brain. This becomes progressively accentuated in passing from the orang, in which the genuflections are the least pronounced, through the chimpanzee to the gorilla, where they stand out in great prominence. As in all primate brains, the parieto-temporal region shows a degree of fissural richness which is the most pronounced. It is, however, in much less striking contrast to the frontal region where the superior, middle and inferior frontal fissures are well outlined. The precentral fissure has become a deep sulcus lying parallel to the central sulcus. In the occipital lobe the transverse occipital fissure is deeper and has an inclination to develop several collateral branches. The lateral occipital fissure is also pronounced. This becomes increasingly the case in passing from the orang to the gorilla, in which latter the occipital

FIGS. 439 AND 440. SIZE AND CONFIGURATION OF THE DORSAL SURFACE OF THE HUMAN BRAIN COMPARED WITH THAT OF PITHECUS RHESUS, THE MACACUS.



FIGS. 441 AND 442. SIZE AND CONFIGURATION OF THE LATERAL SURFACE OF THE HUMAN BRAIN COMPARED WITH THAT OF PITHECUS RHESUS, THE MACACUS.

lobe is much more prominently fissured than in either of the two great anthropoids associated with it. The fissure of Sylvius tends to be more horizontal in its direction, while the fissure of Rolando departs from the superior longitudinal fissure with an angular inclination of something less than 75 degrees. The marked changes in the fissural pattern of the great anthropoids therefore consists in the convolutional richness seen both in the frontal and occipital lobes, with the presence of every fissure found in the human brain more prominently marked than in the intermediate primates, and with marked accessions in the frontal and occipital regions incident to expansion in these portions of the brain.

In man the fissural pattern attains its greatest complexity, so much so that it becomes difficult to identify the several characteristic fissures, which in the lower primate brain stand out in prominence because of the relative simplicity in the sulcal markings. The fissure of Rolando now has an angle of inclination with the superior longitudinal fissure of about 71 degrees; the fissure of Sylvius approaches much nearer to the horizontal than in any of the lower species; the sulcus simiarum has practically disappeared and nothing suggestive of it is to be seen in the human brain unless it be the sulcus lunatus referred to by Elliot Smith as the possible homologue of the sulcus simiarum. The general position of this fissure is marked by the parietal incisure of the occipito-parietal sulcus. The occipital lobe itself shows a richness of fissures generally arranged about the occipital and lateral occipital sulci, which far exceeds in complexity anything observed in the primates below man.

The evidence, therefore, offered by the fissural pattern in the primate brain, especially as it affects the lateral surface of the hemispheres, points to a progressive evolution, starting with a pattern in many respects reminiscent of the carnivore circumsylvian type, and passing from an almost indifferent intermediate stage of the simplest lissencephalic neopallium, through all gradations to culminate in the intricate fissural design of the human brain. There seems to be no single step missing in this gradual transition.

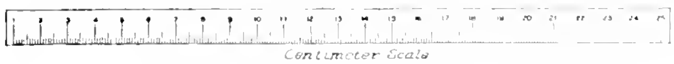
Evolutional Significance of the Cerebral Lobes in the Primate Brain. Nor is this process of gradual expansion confined to the fissures alone. Inasmuch as these landmarks serve to delimit the well-marked physiological areas of the brain surface and thus produce lobation, as a concomitant of the increasing richness of fissural pattern, the lobes themselves become more complicated. In the transitional form of lemur, the identification of the quadrilobular condition characteristic of the primates is difficult, largely because the central sulcus of Rolando is only in an incipient state and the boundaries of the frontal lobe must, therefore, be drawn largely by inference. So also it is difficult to distinguish between the parietal and frontal lobes. But the boundary between the temporal and parietal lobes is fairly well defined by the fissure of Sylvius.

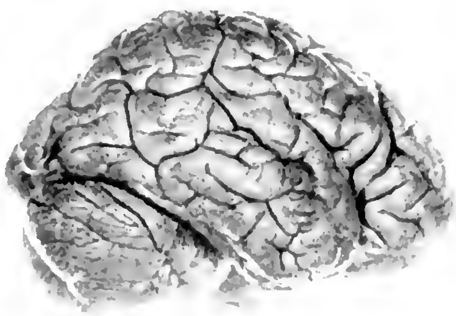
Upon the lateral convexity the evidence of an occipital lobe is almost entirely wanting and such expression as this lobe has is largely confined to the mesial surface of the hemisphere. This observation of the occipital lobe in perhaps its most primitive condition is borne out by the size of the superior colliculi which maintain much of their original proportion and also not a little of their primitive stratification. In tarsius and marmoset, the brains of which are so largely lissencephalic, the difficulty of determining the lobes is equally pronounced. In the absence of any sulcus centralis, no distinct dividing line between the frontal and parietal lobes exists, and only in a general way is the division between the temporal and parietal lobes given by the feebly developed Sylvian fissure. Nothing resembling the sulcus simiarum is present in these brains, although the development of an occipital lobe is much more pronounced than in the lemur, as shown by the fact that the cerebellum is now almost completely covered by the caudal pole of the hemisphere. Thus, starting in the Tarsiodea with an anthropoid hemispheral surface almost free of fissural inscription, it becomes possible, at the next stage in the progressive expansion of the neopallium, to note in mycetes a definite quadrilobular condition in the brain. A well-defined fissure of Rolando separates the parietal from the frontal lobe. A prominent fissure of Sylvius divides the parietal from the temporal, and the incipient sulcus simiarum sets the boundary between the occipital and the parietal regions. Of these four lobes, the most highly developed are the parietal and the temporal, while the expansion in the frontal and the occipital regions seems to be definitely retarded. In the intermediate group of old-world monkeys, the lobation in the cerebral hemispheres upon the lateral surface is so striking as scarcely to need further comment. The tri-fissural pattern in all of these forms produces a decisive quadrilobular lateral surface in which, however, the parietal and temporal regions show the greatest degree of expansive development. This is true not only of the baboon and macacus, but even as much of the gibbon. The lobular development in the frontal region and in the occipital region in these three forms is not pronounced as compared with the temporal and parietal areas, and in none of these is the frontal lobe beginning to assume the prominent proportions which it does in the upper grades of the primate series.

In the three great anthropoids, a quadrilobular arrangement on the lateral surface is distinctly apparent, with evident accessions in the development of both occipital and frontal lobes. It is not, however, until the human brain is reached that the full significance in these changing proportions of the several lobes of the brain becomes apparent. The physiological significance of that expansion, which has been progressively making itself felt in the hemispheres, now becomes more obvious. While the boundary lines between these several lobes of the brain are with more difficulty discerned, because of the greater richness of the fissural pattern and the high degree of complexity of the convolutions, such progress as has occurred affects particularly the frontal and occipital regions. Not, however, that the temporal and parietal areas are less characteristic in their landmarks, but rather that in the process of expansion they have been somewhat overshadowed by the rapid strides of advance made by the frontal and occipital areas of the brain. This advance mostly involves the prefrontal area, which is regarded by the physiologists as representing the seat of such higher faculties as reason, judgment and discrimination. This is the region of the brain wherein those syntheses of neural impulses are assembled which constitute the basis of human experience and personality. It is undoubtedly the case that diseases affecting this part of the brain do much to unseat the process of reason and judgment and have far-reaching effects in changing in one direction or another the personality of the individual. Reference need only be made to the great volume of clinical material already assembled in relation to tumors in the frontal region of the brain, particularly in the prefrontal region, whose outstanding clinical manifestations are marked changes in personality with alterations in the validity of judgment and reason. It is most interesting in this connection to note the tendency of expansion in the frontal lobes among the mammals in what may be considered direct proportion to the development of intelligence. Without pausing here to define too much in detail the meaning of intelligence, it may in general be stated that this attribute indicates the capacity presented by any brain to select between alternative courses of action, that is, to reason and finally form a judgment.

If a number of mammals, those low in the phyletic scale as well as those situated in the upper levels, are contrasted by means of planimetric estimations of the areas on the lateral surface of the brain, and from such measurements planimetric indices are constructed, the following interesting facts are brought to light: The frontal lobe when compared in different mammals shows that the ant eater has a frontal index of 9 per cent, the horse of 13 per cent, the seal of 16 per cent, the leopard of 20 per cent, the brown bear of

FIGS. 443 AND 444. SIZE AND CONFIGURATION OF THE DORSAL SURFACE OF THE HUMAN BRAIN COMPARED WITH THAT OF HYLOBATES HOOLOCK, THE GIBBON.





FIGS. 445 AND 446. SIZE AND CONFIGURATION OF THE LATERAL SURFACE OF THE HUMAN BRAIN COMPARED WITH THAT OF HYLOBATES HOOLOCK, THE GIBBON.

21 per cent, the dog of 29 per cent, the lemur of 23 per cent, the spider monkey 31 per cent, the baboon 31 per cent, the chimpanzee 33 per cent, the gorilla 32 per cent and man 47 per cent. The tabulation from which these indices were computed is given in the appended table. The indices themselves definitely point to the fact that the expansion of the frontal lobe is the goal toward which the entire evolutionary process of the primate brain has been directed.

PLANIMETRIC AREA INDICES OF NEOPALLIUM

Animal	Vernier units		Square inches		Indices	
	Frontal area	T.P.O.* area	Frontal area	T.P.O.* area	Frontal area, per cent	T.P.O.* area, per cent
Man	832.60	965.30	13.3	15.40	47	53
Gorilla	332.00	713.30	5.3	11.40	32	68
Chimpanzee	212.00	441.00	3.4	7.00	33	67
Baboon	176.00	304.00	3.0	6.30	31	69
Spider monkey	106.00	234.00	1.6	3.70	31	69
Lemur	17.60	57.00	0.28	0.91	23	77
Dog	88.60	212.00	1.40	3.30	29	71
Brown bear	102.60	381.60	1.64	6.10	21	79
Leopard	30.00	115.00	0.48	1.84	20	80
Sea lion	166.30	881.30	2.60	14.10	16	84
Horse	173.30	756.60	2.77	11.80	13	87
Ant eater	30.00	100.60	0.34	3.04	9	91

* Temporo-parieto-occipital.

EVOLUTIONAL SIGNIFICANCE OF CONVOLUTIONAL PATTERNS IN THE BRAIN. This conclusion is further borne out by a comparison of the convolutional pattern in the frontal lobe which shows the same trend of development from a relatively simple area, through all the intermediate stages, to the highest degree of convolution seen in the human hemisphere. The obvious purpose of this convolution is to increase the cell-containing substance of the brain and thus to produce a more efficient cellular structure for the transaction of those functions necessary to the regulation of behavior. That the frontal lobe should show the greatest degree of convolutional richness in man is what might be expected in view of his better powers of reason and judgment, his greater ability to profit by experience and his more ample capacity to construct those complex neural syntheses in the constitution of human personality.

By arduous labor and ingenuity, hieroglyphics of several dead languages have been deciphered and their generic relations in linguistic development established. It requires no such effort to interpret the signs inscribed upon the neopallium of the cerebral hemispheres in the primate order. From the simplest fissural inscriptions, through all degrees of elaboration in their increasing structural complexity, their translation reveals a progressive expansion in the endbrain. Such also is the evidence derived from the lobation of the hemisphere with its increasing complexity in convolution. Without hiatus or ambiguity these facts provide a complete record of evolutionary progress in the brain of primates.

Evolutional Significance of the Basal Structures. On the base of the cerebrum, in that portion which comes in contact with the orbital plate of the frontal bone, the process of gradual unfolding is further illustrated. The orbital plate in the lower primates shows a convexity corresponding in position to the orbital socket which produces a concavity in the orbital surface of the brain. As the hemisphere in its frontal area becomes more expanded this concavity decreases. In consequence the orbital concavity is most pronounced in the lower primates. It is a feature of considerable prominence in the intermediate primates, is conspicuous even in the brains of the orang and the chimpanzee, but shows its first marked decrease in the gorilla. Although evidence of it may still be found in the human brain, it is here so inconsiderable that it might fail to attract attention. Associated with the orbital concavity is another notable feature, the *interorbital keel.* This mesial ridge is most prominent in those species with the deepest orbital concavities, and becomes gradually less pronounced as this concavity is gradually decreased by the expansion of the frontal lobe. Through graded stages in the primates the diminution in prominence of the inter orbital keel may be easily traced. It is still a feature in the brain of the orang, and present also in the chimpanzee, although less prominent; it may be discerned, less well defined, in the gorilla, but almost entirely disappears in man due to accessions in all portions of the frontal lobe.

Conditions in the structures related to the olfactory and the optic nerves denote a similar process of frontal expansion. The olfactory bulb and tract in tarsius are much larger than in other primates. Their resemblance to the more primitive rhinencephalic development of carnivores and ungulates is fairly close. The bulb and the tract appear more as an integral part of the basal surface of the endbrain. The lateral and mesial olfactory roots follow their course to their terminations in a manner characteristic of the lower mammals. Progressively, however, in passing upward from lemur, the olfactory bulb and tract become relatively smaller. They are both more easily detached from the overlying orbital surface of the brain, while the divarication of the lateral and the mesial roots of the olfactory tract becomes less conspicuous. The entire development of the rhinencephalon (olfactory portions of the brain) is less prominent and gives evidence of a deflorescence in its structural elements. Accompanying this process there is a diminution in the capacity of olfactory function. In the advance from the lower to the upper end of the primate series a small fissure is found beneath the olfactory tract. This is the sulcus olfactorius, which determines the existence of the gyrus rectus. Both of these features become more conspicuous as the human stage of development is approached. They are both indicative of progressive differentiation in the frontal lobe. These developmental changes connected with the sense of smell are of greatest evolutional moment. Their obvious connotation is a diminution of olfactory sense which gave to the hunting animal its keen scent and to many species a protective accessory in providing warning of the approach of enemies. According to all signs the sense of smell is on the wane in the primates. The archaic rhinencephalon becomes less prominent, the olfactory bulb and tract grow smaller and lose their intimate incorporation in the orbital surface of the brain. Other sense capacities, such as vision, hearing and the sense of touch, the latter especially as developed in the hand and fingers, have replaced the sense of smell by substituting for it receptors both of the distant and contact variety. Dependence upon these latter sensory organs perhaps places the animal in more advantageous relation to its environment, in certain respects at least.

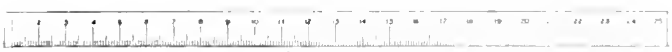
The primordial development of the olfactory sense is preeminently connected with the process of obtaining food. It is conceivable that the constant influx of impulses by this avenue of sensation might be deterrent, if not prejudicial to the further development of other faculties. In the race of life, the procuring of food must always take its place among other objects of much importance to the needs of the organism. It may, of course, be claimed in this connection that the upshot of all action is in the interest of maintaining life. The olfactory sense, therefore, can no more be said to retard the development of such purposes than any other sense. But with the possible exception of that small degree of protective insurance and sexual direction which the olfactory sense provides, its main and decisive influence is connected with the location and identification of food supply. Hence the defloresecence in this department of sensory organization in the primate may be considered as of advantage in developing other and more widely productive courses of reaction.

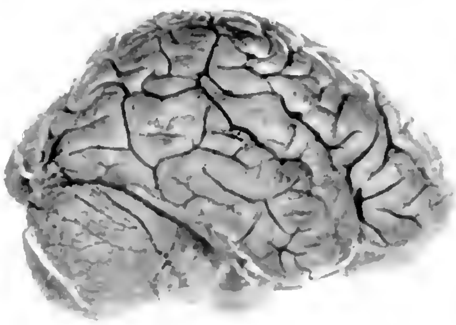
Again the decrease in the olfactory portion of the brain is in direct proportion to expansions in the frontal lobe. It thus appears that, however much the animal may suffer by decreased efficiency in this sphere of sensibility, it gains immeasurably in the combinations of experience made possible through increments to the frontal area.

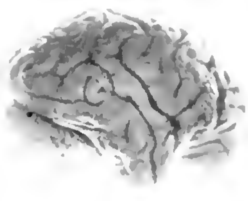
In the case of the optic nerve, a similar record of expansion is to be found. This is seen in the degrees of angulation in the convergence of the optic nerves upon the chiasm and the divergence of the optic tracts from it. This angulation gradually increases in passing from the lemur, through the intermediate primates, to the great anthropoids, and reaches its greatest prominence in man. It is due to the fact that expansions in the head have further separated the eyes from each other. The expansions themselves are due in large measure to the growth of the brain areas above the orbits. Similar expansions in portions of the brain caudal to the optic chiasm are in process and account for the wider angle of divergence in the optic tracts. This feature while far less significant than olfactory development possesses a value, which, however slight, should carry its due weight in estimating the evolution of the brain.

Evolutional Significance of Cerebellar Expansion in the Brain. The influences of expansion may be further discerned in the occipital lobe. This extension likewise affects the lateral lobes of the cerebellum. In the lowest of the primates the cerebellar concavity is a deep impression made upon the basal surface of the occipital lobe by the cerebellum. It is less pronounced in lemur than in higher species because the cerebellum is only in part covered by the occipital lobe. In the marmoset and Hapalidae generally this concavity becomes more prominent, due to the fact that the cerebellum indents the under surface of the brain to a considerable degree, while the occipital lobe entirely covers the tentorial surface of the cerebellum. The cerebellar concavity, and more particularly the postsplenial fossa, is a character observed in all primate brains. The lateral expansions of it become progressively less pronounced in the intermediate primates. It is well defined in the orang and chimpanzee, but becomes less prominent in the gorilla and almost entirely disappears in man where it leaves but a small vestige of the postsplenial fossa to accommodate the vermis.

FIGS. 447 AND 448. SIZE AND CONFIGURATION OF THE DORSAL SURFACE OF THE HUMAN BRAIN COMPARED WITH THAT OF SIMIA SATYRUS, THE ORANG.







FIGS. 449 AND 450. SIZE AND CONFIGURATION OF THE LATERAL SURFACE OF THE HUMAN BRAIN COMPARED WITH THAT OF SIMIA SATYRUS, THE ORANG.

A further change from concavity to something approaching convexity [illegible] surface of the occipital lobe is the result of expansions in the [illegible] in the interest of extending the capacity of visual function.

In still another particular, the cerebellum gives evidence of an expanding process. In lemur the organ is only partially covered by the caudal pole of the brain, due to the fact that the occipital lobe is poorly developed. This condition is characteristic of the more primitive hemispheres in the carnivores and ungulates. Yet even in lemur the tentorial surface has a definitely gabled appearance. The superior vermis is a prominent element, while the inferior vermis appears much more as a surface eminence than in the higher species. In the marmoset, the ultimate primate condition obtains in that the upper cerebellar surface is entirely concealed by the overlying occipital lobe. The tentorial surface also shows a marked gabling with an extremely high prominence in its vermal region. A similar condition exists in mycetes, both on the tentorial and occipital surfaces. In all three of the lower primates, the lateral expansion of the cerebellar hemisphere is relatively slight. The movement toward development in this portion of the brain first becomes evident in the intermediate primates, although even in them the vermis remains a most conspicuous feature of cerebellar organization. It is not until the great anthropoids are reviewed, that the real changes in cerebellar expansion become apparent. In these instances, while the gabling of the tentorial surface is still fairly prominent, there is a distinct tendency for the vermal ridge to lose its high elevation, for the vallecula to become pronounced and for the vermis to fall off in comparison with the lateral lobes. Finally in man, the tentorial surface is almost flat, the vermal ridge inconspicuous and the vallecula so deepened that the inferior vermis is almost lost to view within it. The process which has progressively advanced in the development of the cerebellum is obvious. It is characterized by expansion of the lateral lobes without proportional increase in the vermal portion of the organ. Since the [illegible] represent [illegible] [illegible] this [illegible] [illegible] compared [illegible] [illegible] proportion [illegible] [illegible] [illegible] corresponding [illegible] muscles.

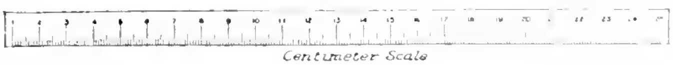
EVOLUTIONAL SIGNIFICANCE OF [illegible] IN THE B[illegible] PRIMATES.—In many details [illegible] differentiation. The features [illegible] [illegible] This system is important from the fact [illegible] influences of the neopallium. It brings [illegible] combination which [illegible] activity [illegible] selective opportunity. The evidence of [illegible] the presence of three prominent structures [illegible] [illegible] system, the pyramidal [illegible] At the [illegible] extremity of the series all three of these structures [illegible] Employed as a key to the [illegible] animal [illegible] [illegible] capacity. In many respects the [illegible] pyramidal [illegible] Proceeding [illegible] [illegible] [illegible] pyramidal [illegible] pons Varolii is a more protuberant structure. The cerebral peduncles attain greater definition and size, while structural differentiation in the base of the brain stem reaches its full development in man. The increasing size of the pyramid, of the pons and of the cerebral peduncle seems to indicate the final development of new motor capabilities made possible by manual specialization. Man and all his works are epitomized by these structures of the brain. Without them there would be neither reason nor opportunity to discuss the achievements of mankind. Too great importance, therefore, cannot be laid upon this specialization, which has progressed through certain preparatory stages of quadrumanal differentiation, and finally attained its definitive manual development.

But lest over-much emphasis be attributed to the hand *de ipso*, it must be borne in mind that no such development could have occurred had not an almost equally important specialization affected the lower extremity. The structural standard of the human upper extremity insists upon certain proportions in the length of the arm, forearm and hand in relation to the rest of the body. It also prescribes definite intrabrachial relations of the arm to the forearm, the forearm to the hand, and the hand to the fingers. This human standard seems essential to the most perfectly differentiated upper extremity. Yet it is a fact that many of the lower apes come nearer to this standard than do the anthropoids standing nearest to man. This is notably the case in the orang, in the chimpanzee and in the gorilla. In them the upper extremity is out of all proportion with the human standard. In the three great anthropoids, the arm, forearm and even the hand are too long for the most flexible adaptability. The limitations of adaptive range of motion imposed by this excessive length have been noted in recounting the behavioral activites of the higher anthropoids. The fact that the fingers almost touch the ground when the animals stand in the erect position shows in what respect these members are limited in the accomplishment of skilled performances near to the body. These impediments are also pronounced for projectile activities, for the wielding of weapons or the manipulation of instruments. The upper extremity in the great anthropoids is preeminently specialized in the interest of arboreal life. Its enormous musculature and great length favor the exigencies of locomotion determined by tree climbing. Some other factor, therefore, over and above the actual specialization of the hand, must serve as an important incentive for the expansion of the cerebral cortex, which led to its ultimate expression as seen in the human brain. Were this not the case, it is probable that some of the lower simians would possess brains more closely in harmony with that of man than the great anthropoids. It is probable that this primary factor is to be found in the foot rather than in the hand.

The lower extremity, which specializes a foot of preeminent hand-like character, has manifested this differentiation essentially in the interest of arboreal life. Such life definitely restricts the motor capacities of the animal by consigning it to a type of locomotion for which the use of both hands and feet is indispensable. Under the circumstances, however much the proportions of the arm, forearm, hand and fingers may correspond to human standards, complete manual differentiation is impossible. The hand, to be the freest for the purposes of manual manipulation, must be permitted to operate on a basis far more secure than that offered by arboreal life. In other words, the animal, to make the most perfect use of the hand, must, so to speak, stand with both feet upon the ground, and from this point of vantage, be able to traverse and utilize at will all of the habitat zones of life. The adequate structure for securing such a basis of operation is not to be found in the hand-like specialization of the foot. None of the apes, for example, could in any wise adjust itself to life upon the earth so that it might effectively take advantage of other habitat zones. It is undoubtedly the hand-like specialization of the foot in the great anthropoids and in all of the lower primates that has committed these animals to the relatively low level of differentiation attained by them. *For this reason they are still apes.* It seems impossible to escape the conclusion that the evolution of a human foot eventually freed the hand for all the complex purposes to which it has been applied. The development of this foot doubtless had its inception in some pedal structure specialized for arboreal life. The main factors producing the modification were eversion and elongation of the foot, formation of a broad supporting plantar surface, loss of prehensile functions in the great toe and distal migration of the hallux. It is generally believed that such development of the foot is of primary importance in furthering the assumption of the erect posture, and thus eventually leading on to all of the extensive modifications necessary to the development of the human hand.

The following stages of postural evolution passing from the quadruped to human bipedal locomotion are based on the critical analysis of Gregory and Morton. Those gradual changes which finally gave rise to the human foot had their inception in the Eocene. They were first manifest in some terrestrial quadrupeds, which in the course of certain behavioral readjustments began to live in the trees. This arboreal life imposed upon them new necessities in locomotion. It had most pronounced effects upon the fore- and hindpaws. In order to climb and move along the branches, a clawing grip was necessary for this clinging type of transit. Long, sharp claws developed in consequence of such adjustment. The digits of the manus were short. The palm of the hand was well padded. The pollex was short, but not opposable. There was as yet no squatting or half-sitting posture. The toes were also short and clawed, the heel elevated, the plantar surface of the foot was padded and the great toe well developed. These arboreal quadrupeds had, however, made but imperfect adaptation to tree life. Their movements were slow and their range of activity correspondingly limited. The tree shrew is a living representative of such subprimate quadrupeds, while certain Eocene

FIGS. 451 AND 452. SIZE AND CONFIGURATION OF THE DORSAL SURFACE OF THE HUMAN BRAIN COMPARED WITH THAT OF TROGLODYTES NIGER, THE CHIMPANZEE.



FIGS. 453 AND 454. SIZE AND CONFIGURATION OF THE LATERAL SURFACE OF THE HUMAN BRAIN COMPARED WITH THAT OF TROGLODYTES NIGER, THE CHIMPANZEE.

primates of this type have been described from fossil remains by Professors Matthews and Gregory.

The next locomotor adjustment came with the advent of light lemuroid primates, whose locomotion was still of the slow, cautious, climbing type, which depended upon a clinging, clutch-like grip. All of the digits of the manus became longer, but the outer two were especially elongated. Similar modifications affected the foot, so that the entire adaptive change established a strong quadrumanal tendency. Pedal fulcrumation was still of the tarsal form, while both hallux and pollex were well developed. Modern examples of this stage are found in loris and potto.

A more decisive advance made its appearance when arboreal locomotion combined the advantages of climbing with leaping. Passage through the trees now became swifter and more effective. A tendency to semi-erectness soon developed, and the squatting posture was well established. The digits, metacarpals, tarsus and metatarsals all elongated, giving the quadrumanal differentiation still greater prominence. Fulcrumation advanced to the metatarsus, thus permitting of a greater leverage in the take-off for leaping. The hallux and pollex were more powerful and definitely opposable. The forms most representative of this stage are lepidolemur and notharctus; with these should be included the leaping tarsioids, and especially the Indrisinae.

From leaping and climbing it was but a short step to the stage of swinging cursorial locomotion through the trees. At this time brachiation was first introduced, and had its far-reaching influence upon all subsequent development. Swinging by the hands from branch to branch naturally lengthened and strengthened the arms. The manus developed a suspension grip which caused the digits to elongate, although the thumb underwent reduction, or else, as in the spider monkey, did not appear at all. The foot developed a grasping grip, and all of its elements elongated. Pedal fulcrumation was metatarsal. The semi-erect and sitting postures were still further emphasized by these changes and ischial callosities appeared in consequence of habitual squatting. The foot maintained digitigrade tendencies, although the heel touched the supporting surface in locomotion, but did so after the toes made their contact. The timing formula in this respect was *toe-heel*, as in the previous phases. The lower extremity despite its increased length still presented its pelvic flexion. This stage is represented by the Cebidae and the old-world monkeys except most of the baboons, whose aberrant cynomorphous specializations produced a quadrupedal reversion with shortening of the limbs, fingers and toes in adjustment to living on the ground.

All of these modifications possibly occurred in the earlier portion of the Oligocene. Late in this geological era the primate stock took a great stride forward. Locomotion was still predominantly brachiating in type. The manus retained its suspension grip which produced elongated digits, but a rudimentary thumb. The latter, however, was opposable. The tail disappeared and the foot developed a grasping grip. The legs became extended on the pelvis, thus reducing the primitive pelvic thigh-flexion, and rendering the ancient type of quadrupedal locomotion impossible. This modification at once advanced the cause of the erect posture. It did far more, however, by introducing the first phases of bipedal locomotion which, notwithstanding its awkward and ineffectual nature at first, created the structural pattern essential to the culminating differentiation of the human foot.

Among living species the beginning of the Hylobate branch (gibbons) clearly marks this critical departure. The orang-outang is probably an offshoot from this stage, while *Dryopithecus* carries the stage directly upward. Early in the Miocene there came a great increase in body weight which particularly affected such primates as possessed this newly acquired orthograde tendency. The greater weight brought the animals nearer to the ground, and thus determined certain terrestrial specializations. Arboreal locomotion was [illegible] in type. The arms became extremely long and powerful—longer and more powerful, in fact, than the legs. Erectness was further increased because the thigh was more extended upon the pelvis. Standing and walking upright manifested definite improvements. Under these conditions the toes and heels touched the ground simultaneously, although the timing formula was still infrahuman in type. In arboreal locomotion, the foot still retained its grasping grip with shortened digits but opposable hallux. This is true of all the great apes with the exception of the orang, which developed a suspension grip in the foot due to its more strictly arboreal life. Adult gorillas, especially the older males, have definitely ground-gripping feet with broad heels, flat arches and plantar eversion with some distal advance of the great toe. Their pedal fulcrumation is well forward in the metatarsus. Arboreal locomotion in all three of the great apes is predominantly brachiating. This development imparted to the upper extremities those specializations which maintained the hands as part of the locomotor apparatus and thus impeded their most effectual manual manipulation. The manus retained its suspension grip well marked in the orang and chimpanzee, but showed evident decline in the gorilla whose increasing tendency was to assume a terrestrial habitat. Thus, however strong the incentive toward terrestrial life may have been in the great apes, that inherent arboreal commitment set upon the primates in early Eocene times still kept them true to all their rigid simian inheritance. To be more than apes it was necessary for them to shed that stigma which tree life stamped upon them. This [illegible] apes never accomplished. The experimental efforts evident in [illegible] anthropomorphous tendencies at length found a new opening. It was the [illegible] the foot, producing a supporting structure having a well-[illegible] non-opposable hallux, and a heel-toe timing formula in [illegible]. At some later period in the Miocene the two great branches of the [illegible] parted company. The structural decision at this juncform was a critical one. Both the apes accepting the trees [illegible] man, because of his true human feet and what they supported, [illegible] acquired the earth with all it contained. Thus, with [illegible] the past, with a true ground-gripping foot and plantigrade [illegible] then, with longer legs and actual erectness for effective transportation, the hands were finally liberated for the purposes of human success.

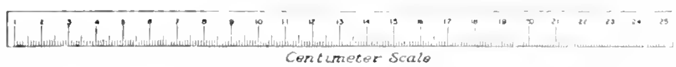
The specialization of the human foot, which must have [illegible] through great periods of time, marks the decisive parting of the ways between the apes and the human family. For however permissible it may be to regard the upper extremity, and especially manual differentiation, as the most cogent influence affecting the expansion of the brain and cranium, the hand itself was ultimately dependent upon the differentiation of human feet. Nor is it possible to omit all of these factors in structural organization which finally made possible the erect posture, setting the head upon the shoulders so that the eyes might look forward and upward and the hands follow the direction of the eyes.

Upon the dorsal surface of the brain stem, the record of progressive expansion may also be discerned. Apart from the conspicuous evolutional features in the cerebellum, expressed especially in the pronounced expansion of the lateral lobe, this region of the brain contains other elements equally significant, if less conspicuous. The progressive increments in the clava and cuneus, those structures in the dorsal sensory field representing the sensory inflow from the upper and lower extremities, have already been discussed in their functional aspects. That both of them should enlarge in passing from the lower primates, through the intermediate groups, to man, has its explanation in the augmented stream of afferent sensory impulses from the deep proprioceptive structures of the body. Fluctuations in the interrelations between the clava and the cuneus are of even greater moment. In the lower primates it is the clava which shows more prominence. Reaching impulses from the lower extremity and tail, it has an extensive sensory field to serve in its capacity as relay station. The cuneus is concerned with the influx from the upper extremity. In certain of the lower primates, more particularly in those which possess a highly developed prehensile tail, this disparity between the clava and the cuneus is most pronounced. In such species, the column of Goll is larger than that of Burdach. This augmentation is in fact signalized by a special element, known as the nucleus of Bischoff. The Bischoff nucleus makes its appearance only in those animals possessed of a prehensile tail or one specialized for direct participation in locomotion. The subsequent disappearance of this median unpaired nucleus, and the gradual loss of the clava's preponderance over the cuneus, with the involution of the tail, is a matter of much evolutional significance. The clava actually becomes less prominent and smaller than the cuneus in the intermediate primates. The disparity is more marked in the gibbon, which has no tail, and in which the upright posture is but tentatively and occasionally assumed. The progressive emphasis of appendicular specialization, imposed by the development of the hand, completes the supremacy of the cuneus in the sensory field. This final predominance of sensory areas for the hand has a more far-reaching effect than its influence upon the sensory sphere alone. The richness of all motor specialization rests necessarily upon a substratum of sensory apperception, in order that the kinesthetic associations, built up in connection with each newly acquired motor performance, may be adequate to direct its execution and to reconstruct its formula for future repetitions.

Evolutional Significance of the Development of the Special Senses. If there is much to indicate the waning of olfactory sense, as various anthropoid stages are traversed in approach to the ultimate conditions in the human brain, so also there is evidence of a vast change in two other realms of special sense. In the case of olfactory sensibility, the process is one of actual involution. With sight and hearing the matter stands otherwise. Here the primitive centers in the midbrain recede but transfer their functional offices to more expansive areas in the cortex of the endbrain. This telencephalization favors further enrichment in the realms of sight and hearing. The gradual diminution in the size of the mesencephalic colliculi furnishes the structural indication of this process. The transference of functions from an area formerly prominent as the optic lobe of the midbrain entered upon its initial stages in the earliest mammals. Even in the lowest of the primates, the lemur, the marmoset and the tarsius, both sets of colliculi manifest a degree of prominence which suggests the retention of some primordial function. Both collicular prominences appear to be still active to a large extent in the functions of sight and hearing respectively. This is particularly true of that range of auditory and visual activity which concerns itself with immediate reflex reaction, thus offering the animal a greater margin of safety. However notably this may apply to the sense of hearing, it is also the case, perhaps to a less marked degree, with reference to vision. From the lower primates upward, a definite decrease in the prominence of the colliculi indicates a larger measure of functional participation by the higher auditory and visual centers. Evidence of their primitive importance may still be elicited from collicular eminences even in man. This is recognized in the well-known phenomenon when a sudden, unexpected noise may cause the individual to start or to come to an abrupt halt. Similarly, a flash of light before the eyes may produce all of the reactions of primitive defense. But responses such as these represent vestiges of more extensive reactions formerly administered through the primordial centers for vision and hearing. Sounds and visual stimuli are in the main treated with deliberation, as the result of cortical elaboration. The progressive decrease in structural prominence of the mesencephalic colliculi, taken in conjunction with the expansion in the occipital portion of the cerebral cortex, supplies the evidence of an evolutional process, than which there is no more decisive example in the whole realm of organized matter.

Evolutional Significance of the Epiphysis Cerebri in the Primates. Another side of the collicular deflorescence of the mesencephalon may perhaps be touched upon somewhat tentatively, but not without a sense of growing confidence as time develops more ample understanding of the important structures known as the endocrine glands. The cephalic extremity of the longitudinal intercollicular sulcus in the primate series tends to become broader and flatter, forming a comparatively roomy fossa at the cephalic extremity of the midbrain. In this depression rests a specialization of the diencephalic roofplate, the *epiphysis cerebri*. This structure has a long and complicated history from the beginning of vertebrate specialization. In its earliest representation it makes itself apparent in a highly specialized form and gives rise to a pair of eyes situated in the middle of the forehead. This is the primordial condition of the epiphysis cerebri in the cyclostomes. After many fluctuations in passing through the selachians, ganoids and teleosts, in which it manifests a general retrogression from its sensory specialization, it shows some tendency to develop in a glandular direction. Then it appears in the amphibians once more as a highly differentiated distance receptor, apparently for the perception of light. In some of the lower reptiles it becomes even more highly specialized as, for example, in the parietal eye of sphenodon. In the bird it takes form as a complexly organized gland whose special ducts distribute its secretion directly into the cavity of the third ventricle. In the mammals, however, its development is otherwise. Only in the earliest stages of ontogenesis does it show tendencies toward glandular differentiation, and thereafter undergoes degenerative changes. In man, in later life, it gives evidence of advanced degenerative change characterized by the deposition in it of a sand-like substance, known as acervulus cerebralis. In early stages of human development,

FIGS. 455 AND 456. SIZE AND CONFIGURATION OF THE DORSAL SURFACE OF THE HUMAN BRAIN COMPARED WITH THAT OF GORILLA GORILLA.



FIGS. 457 AND 458. SIZE AND CONFIGURATION OF THE LATERAL SURFACE OF THE HUMAN BRAIN COMPARED WITH THAT OF GORILLA GORILLA.

Explanatory Note to Figure 459

The several horizons of cerebral development indicated by the figures on the opposite page require some further comment with reference to their evolutional significance.

I. The Lemuroid Horizon is here considered the basic primate level. It contains many brain features, still in the crude, which become dominant in later development. It also illustrates such hesitations and indecisions as might be inherent in a momentous transitional stage. Faintly, at least, it shows the first feeble impressions imparted to the brain by adaptation to arboreal life and indicates the general lines of cerebral advance consequent upon tree-living habits. (Tarsius and Lemur.)

II. The Simian Horizon illustrates the definite crystallization in cerebral architecture of those structural features which result from the adaptations to arboreal habitat. It clearly reflects the attainment of quadrumanous specialization, at the same time disclosing the effects of certain restrictive influences, such as pronograde locomotion and the as yet partial liberation of the forelimbs from locomotory function. (Old and New World Monkeys.)

III. The Proanthropoid Horizon is epochal in its effects. A new type of adaptation has reorganized the proportions and postures of the entire body. Brachiation is now substituted for a pronograde locomotion in which latter the upper surfaces of the branches are grasped by the handlike fore and hind extremities. Swinging from the branches, as do the Gibbons, has produced a marked elongation of the hands, arms and trunk. It has further caused the body to assume a more perpendicular position in passing through the trees and a real erect posture upon the ground. The Gibbon can in fact stand, walk and run upright. It has, in addition, lost its tail, due undoubtedly to its well-established habit of sitting upright in true anthropoid fashion. The animal is, nevertheless, much inferior in its cerebral organization to the higher anthropoid apes and is hence regarded as a representative of that proanthropoid stage whose arboreal readjustments laid the foundations for the development of the great apes and man.

IV. The Anthropoid Horizon shows a further specialization in the direction of the ultimate erect posture of man and the final freeing of the hands for purposes other than those of locomotion. Arborealization still exerts such a potent influence upon all of the three great apes, that their advances in the direction of anthropoid specialization are definitely restrained by this factor. While all of the three great apes, Orang-Outang, Chimpanzee and Gorilla, habitually walk in a modified pronograde manner, using the knuckles of the extended hand for support in walking and running, these animals are capable of standing, walking and running upright. The erect posture, under these circumstances, has little of the perfection attained by man. It is both ineffectual and ungainly. Running and walking are done with a shuffling, waddling gait, with a tendency to come down upon all fours whenever speed is necessary. The great weight of the anthropoid apes has enforced upon them an arboreo-terrestrial mode of life. This is more particularly true of the Gorilla which, although it does not resort to anything approaching brachiation in its arboreal locomotion, does employ its massive arms for reaching up to the branches, thus drawing itself upward from the ground. All three of the great apes appear to be offshoots from the proanthropoid stem; while still another offshoot gave rise to the races of men.

V. The Human Horizon demonstrates certain anthropomorphous conclusions which were first suggested in the proanthropoid stage. Effectual erect posture is at length attained, the hands liberated from purposes of locomotion, speech acquired, and the frontal area of the brain greatly expanded. The primate tendency so obviously introduced on the Lemuroid Horizon has, under the influence of arborealization, progressed to a proanthropoid stage whose essential contribution is the inception of the erect posture. Two major lines of anthropoid derivation induced the adaptations which led respectively on the one hand to the great apes and on the other to man. Whether the anthropoid stem was a separate offshoot from the proanthropoid level, or whether several such offshoots developed, is still a question. The morphological constituents of the brain strongly suggest that the departure of man from the proanthropoid level was at first by a stem in common with the Chimpanzee and Gorilla, with subsequent bifurcation leading to the wide divergence between the human and his neighboring coordinates among the great apes.

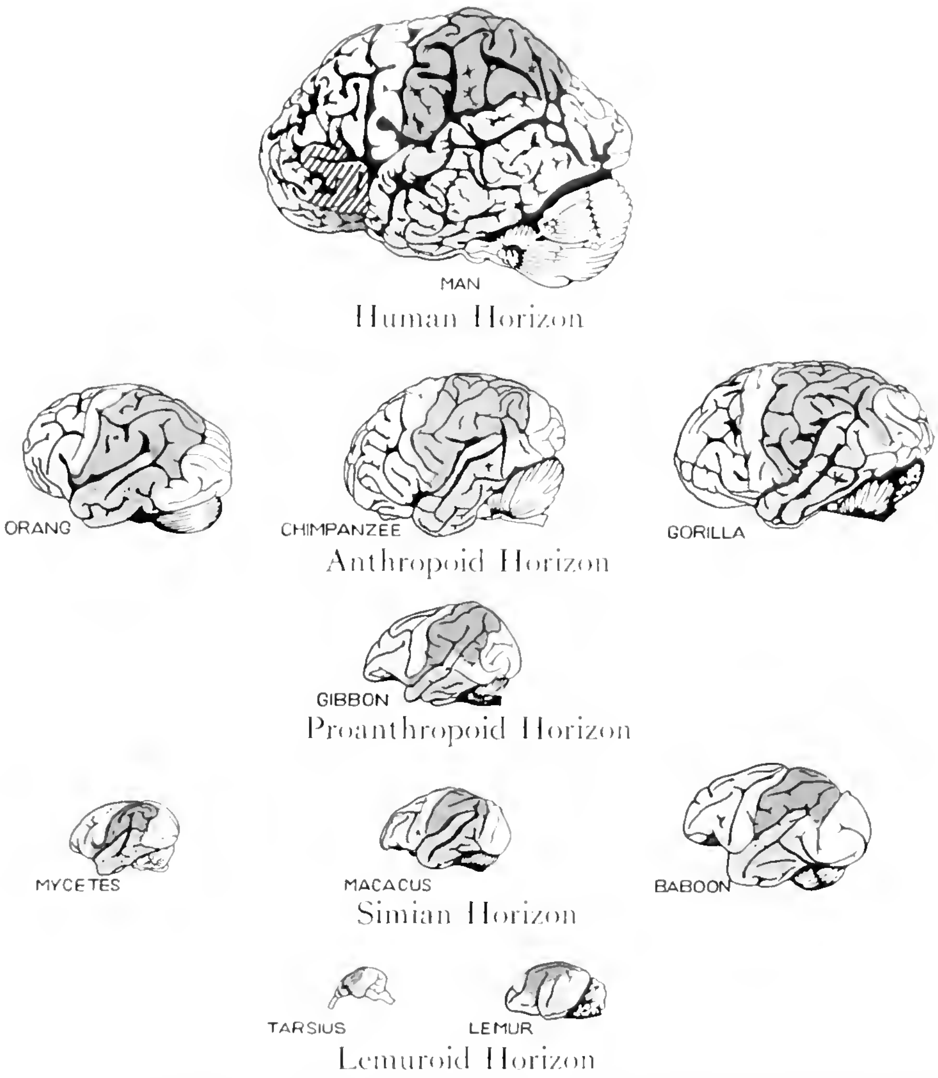


FIG. 459. PRINCIPAL PRIMATE HORIZONS, SHOWING THE EVOLUTIONAL EXPANSION OF THE NEOPALLIUM.

The original drawing reproduced the actual size of each brain depicted; in this figure each brain is reduced to two-sevenths actual size. The progressive expansion of the psychic area (blue) is clearly demonstrated in ascending from tarsius to man.

KEY: Blue, Psychic Region; Red, Motor Region; Green, Sensory Region; Yellow, Visual Region; Gray, Auditory Region; Red and Blue, Speech Area.

especially in fetal and infantile life, the pineal body has much the appearance of a glandular structure. There seems fair probability that it is actually a gland which contributes its secretion directly to the blood in these periods of life. It has been maintained that its function is to check the development, not only of the rigid skeleton, but also of sexual differentiation and maturity. If destroyed by disease, these inhibitory qualities are lost and precocious development of body stature with premature differentiation of sexual activities result. This, in fact, is the clinical syndrome, well recognized for nearly a quarter of a century and known as *macrogenitosomia praecox.*

These and many similar facts would indicate a functional activity on the part of the pineal gland. Whatever claims may be urged for it in regard to the specialized inhibitory function, which it exerts upon the maturation process in development, should not be accepted without much reservation. There is great room for improving our understanding both of the structure and the functional activity of this portion of the nervous system. It is of interest, however, that the size of the pineal fossa progressively increases from the lowest of the primates to man. This indicates, no doubt, that the pineal gland itself correspondingly increases in size, and thus adds to the process of growth a decisive inhibitory factor which holds in abeyance the development of maturity in the human race. It is noteworthy in this connection to recall the pertinent note made by Alfred Russell Wallace concerning the baby orang-outang which he once captured and observed. In his efforts to ameliorate the discomforts of infancy, which this orphaned orang suffered, he placed with it, as companion, a young macacus monkey of about equal age. The great disparity in their reactions was apparent at once. The lower primate, although an infant, showed almost all of the activities of the adult. It was constantly in search of food on its own initiative and not in any way embarassed by the fact that it had been deprived of maternal care. The young orang, on the other hand, lay continually upon its back as might a human infant, quite as helpless to care for itself and most imperfectly developed even in its simple motor activities. Here, apparently, in one of the higher anthropoids, was demonstrated that tendency to retard functional differentiation, in order to obtain the advantages of a long period for maturing. That this great anthropoid shows a period of latency in development almost as long as the human infant is most significant. The phylogenesis of the pineal gland lends weight to the theory that it may and does become specialized as a glandular structure, contributing its secretion to the blood stream. That it acts in the capacity of holding in abeyance the development of statural and sexual differentiation is still somewhat in the conjectural stage. This theory is advanced with all the hesitation that should naturally attach to a hypothesis still but imperfectly substantiated and not having as yet attained universal acceptance.

SUMMARY

A survey of all these facts concerning the primates amply justifies the presumption that this group of animals presents a constancy in brain development by which they may be distinguished from all others. Even more significant are the progressive modifications affecting the fundamental design of the primate brain. Nor can there be any doubt that throughout the entire process of this increasing complexity, the structural pattern of the brain has shown its progressive modifications in harmony with progressive adaptations in the behavior of the primates. Many long periods of structural design, many protracted eras of behavioral trials preceded the final production of a brain capable of all the powers which distinguish man.

Chapter XXX

THE INTERNAL STRUCTURE OF THE BRAIN STEM OF THE PRIMATES, ITS EVOLUTIONAL MODIFICATION IN RELATION TO THE DEVELOPMENT OF BEHAVIOR

Essential Similarities in Internal Elements

THE external appearance of the primate brain may be sufficiently conclusive of the evolutional process in this order of mammals. Surface appearances, however, are often deceptive. The intimate internal organization of the brain may even disqualify the conclusions based upon superficial survey. If, on the other hand, the evidence of the internal structure corroborates that offered by the outer surface, the testimony becomes doubly convincing.

Concerning the similarities of organization in the primates, cerebral architectonics yield an embarrassment of riches. The homologous correspondence of each particular is pronounced beyond question of doubt. Only in the early transitional stages from lower forms of mammals to the primate kind, might there be room for dispute. A review of the brain stem in the lemur, or even in the marmoset, may seem to justify the objection that the internal structure is not sufficiently specific to distinguish it from some relatively lower mammal. Even under these circumstances, more extended inspection of the chief diagnostic features in the brain could not fail to reveal effectual differential characters. No such objection may be raised in connection with the intermediate primates or with those constituting the group of higher anthropoids. In fact, real difficulties might be experienced in distinguishing between the identifying characters of the human brain and the homologous structures in the brains of gorilla, of chimpanzee or of orang. A close scrutiny, however, discloses definite structural variations which differentiate between man and the great apes.

In their size, position, relative proportion, general disposition and topographic relations, the following constituents justify the assumption that the primates represent an organic aggregation, which is harmoniously integrated by unmistakable ordinal characteristics in the brain: The inferior olivary nucleus, the pyramid, the pontile nuclei, the cerebral peduncles, the superior cerebellar peduncles, the dentate and red nuclei, the dorsal sensory nuclei, the nuclei of Deiters and Schwalbe, the substantia nigra, and the superior and inferior colliculi of the midbrain.

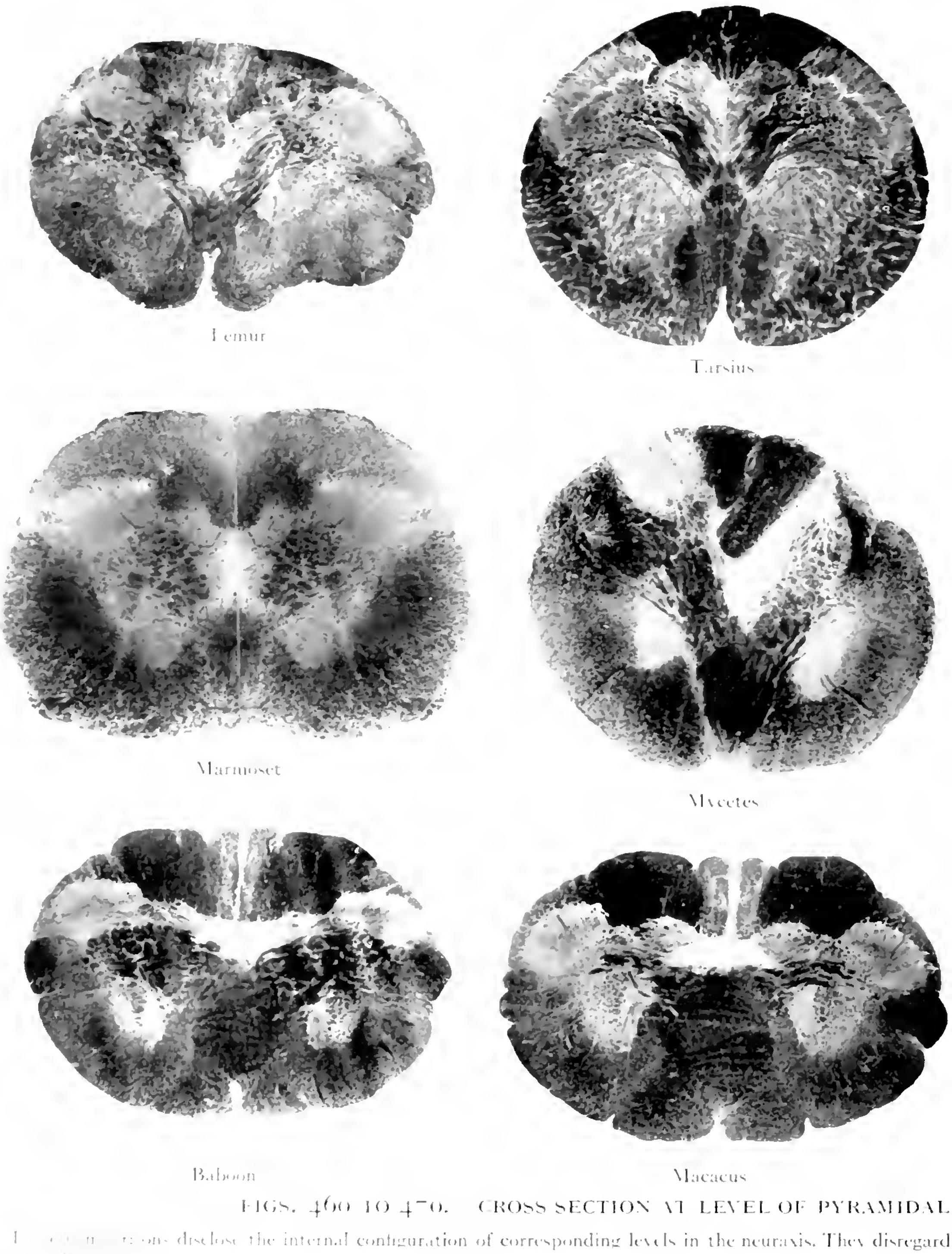
EVOLUTIONAL MODIFICATIONS IN ARCHAIC STRUCTURES IN THE BRAIN OF PRIMATES

Although there is some difference in the emphasis with which the archaic elements of the brain disclose the process of evolution when compared with more plastic, impressionable structures, the ancient constituents none the less reveal the effects of adaptive modification. The steadily advancing clearness of definition, manifested by such archaic elements as the cranial nerve nuclei, is impressive. There appears to be a progressive sharpening of outline which determines the locus of these nuclei. Such nuclear aggregations, for example, as those of the hypoglossal nerve, which innervates the muscles of the tongue, show increasing distinctness in their boundaries with the assumption of a more definite nuclear individuality.

Adaptations in Hypoglossal and Facial Nuclei. The hypoglossal nucleus slowly emerges from the maze of an indefinite cellular collection until it has all the distinctive characteristics of a circumscribed governing center. In similar manner, the nucleus facialis shows marked accessions in nuclear individuality, attaining its sharpest outline in the human brain. This nucleus is of great interest because it has not in the main all of those archaic characters inherent in most of the cranial nerve nuclei. The muscles of facial expression are essentially a mammalian development, and the nucleus facialis is therefore, in part at least, a cellular specialization of relatively late appearance. Since it innervates those structures of the head and face involved in emotional expression, its greatest functional capacity occurs in those forms having the most extensive range of emotion. The facial musculature is also engaged in the acts of swallowing and mastication. Not a few of the primates develop large cheek pouches in which they retain masses of food, awaiting later deglutition. During mastication the vestibule of the mouth, between the teeth and the cheeks, is compressed in order to bring the food between the grinding surfaces of the teeth. The lips during this process also are drawn together, and thus play an essential role in mastication. During the act of swallowing, the cheek recesses of the vestibule are likewise occluded and the lips compressed, so that the bolus of food is forced backward from the mouth to engage between the pillars of the fauces. This masticatory and deglutitional element, innervated by the facial nerve, represents its primitive and basic function. The innervation of the muscles of expression, for portraying states of emotion, is a newer functional attribute of the facial nucleus. As a direct effect of the expansion in emotional expression, the nucleus facialis reaches its highest organization in man.

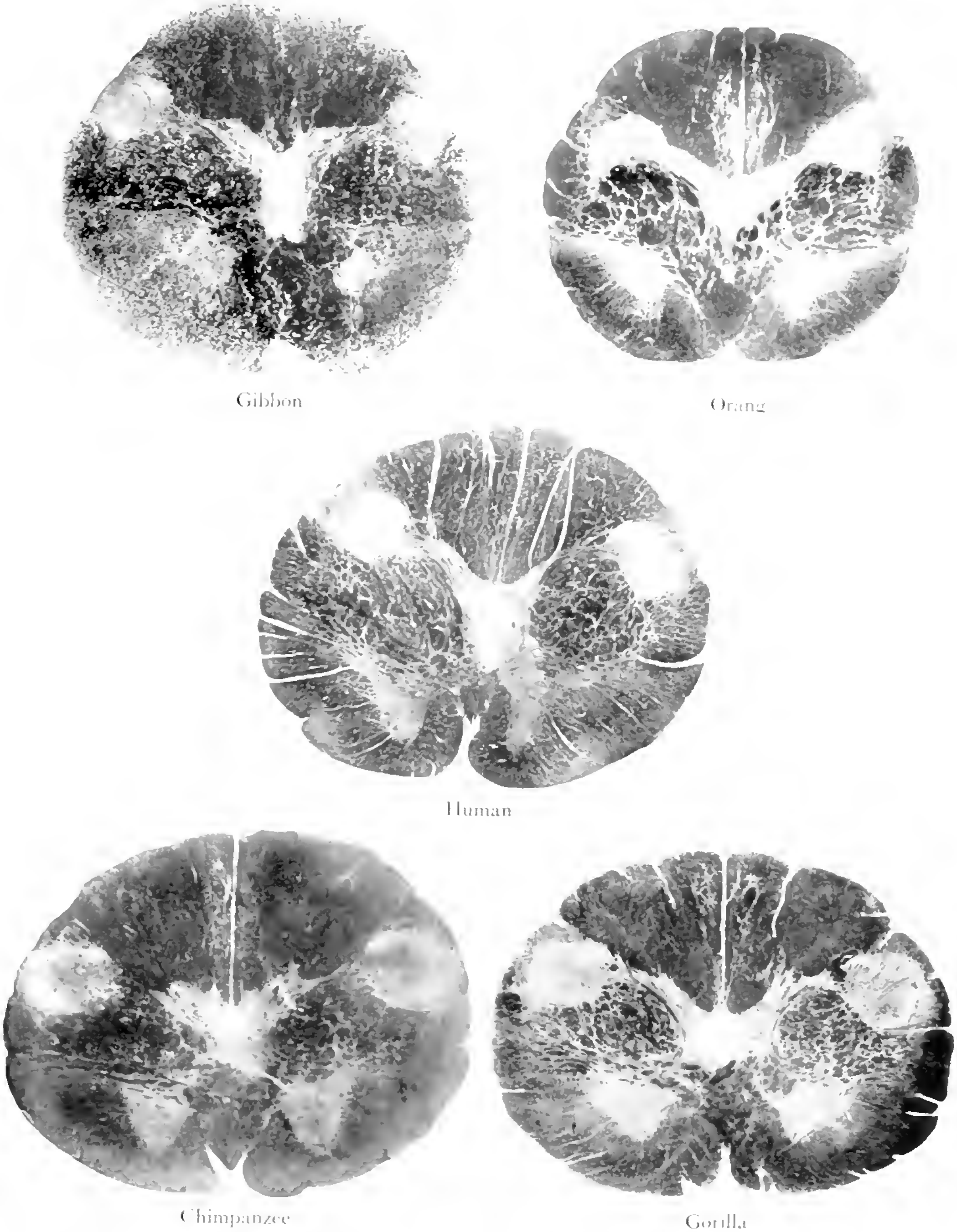
Adaptations in Masticatory Nucleus and Reticular Formation. A like process of increasing distinctness applies to the nucleus masticatorius which has an even greater antiquity. Many vicissitudes have affected the sensory portion of the trigeminal nerve, but its motor division has remained constant.

Progressive increase in the definition of the oculomotor nuclei, including the nucleus abducentis, the nucleus trochlearis and the nucleus oculomotorius, may be observed in passing from the lower primates, through the intermediate stages, to the great anthropoids and man. Nor is this tendency confined to the cranial nerve nuclei. It is also conspicuous in the reticular formation of the entire brain stem. The exact degree of progressive delimita-



FIGS. 460 TO 470. CROSS SECTION AT LEVEL OF PYRAMIDAL

[illegible] disclose the internal configuration of corresponding levels in the neuraxis. They disregard [illegible]

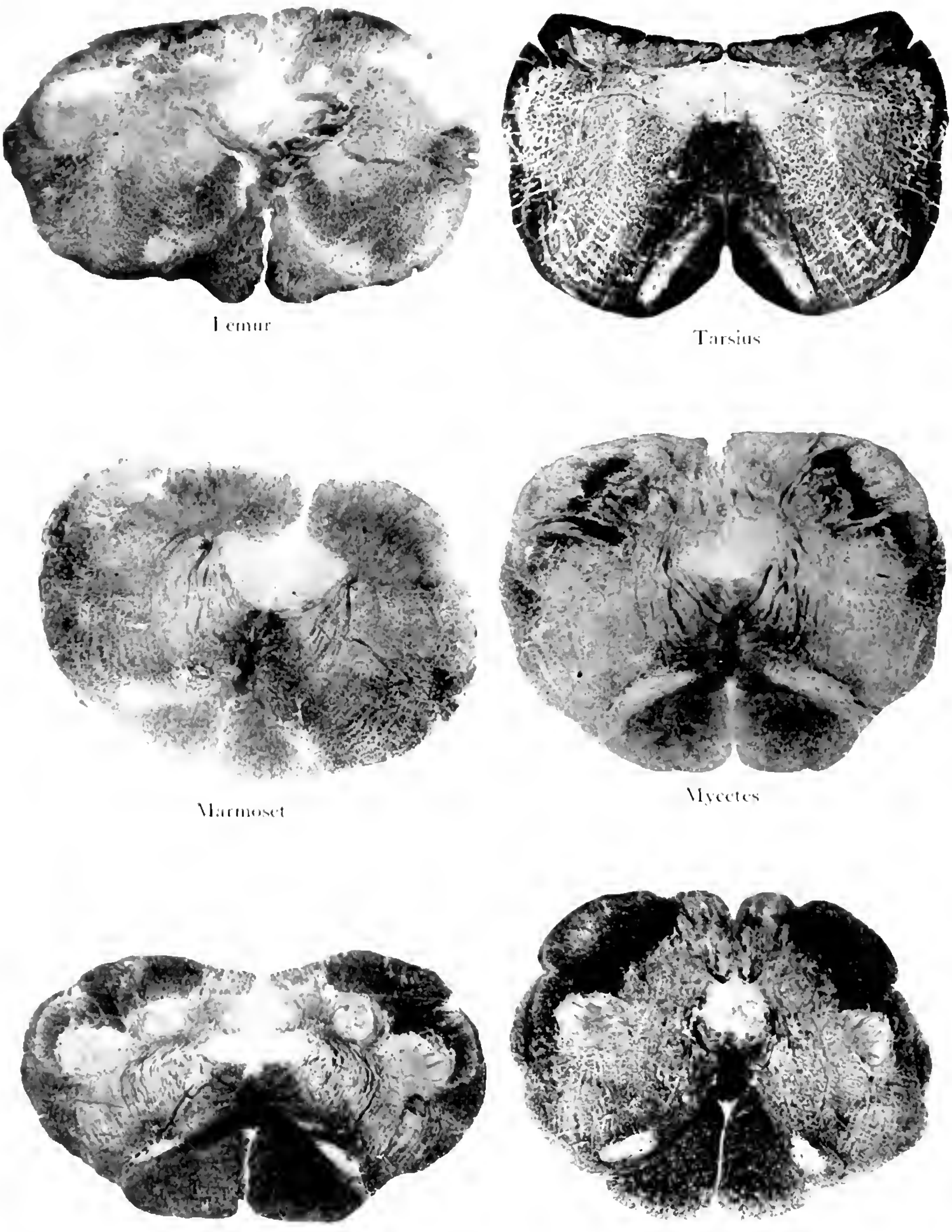


DECUSSATION IN THE COMPARATIVE PRIMATE SERIES.

the actual dimensions of the sections. Such measurements are given in the description of each level in the tion of outline in the formatio reticularis defies estimation by means of mensuration or other methods of precision. Its comparison in the various species of the primates conveys the impression that this diffuse mass of gray and white matter becomes more clearly defined in ascending the primate series. This effect may be the result of increasing sharpness in definition of such nuclei as constitute the origin of the cranial nerves, or due to the fact that certain important nuclear masses, such as the red nucleus and substantia nigra, gradually emerge from the indiscriminate matrix of the reticular formation. Such increasing definition within the formatio reticularis is a morphological tendency clearly demonstrable in the brain stem. It should not be passed over without due notice of the fact that even the diffuse matrix of this structure does not escape the influences of that progressive specialization affecting other ancient parts of the central nervous system.

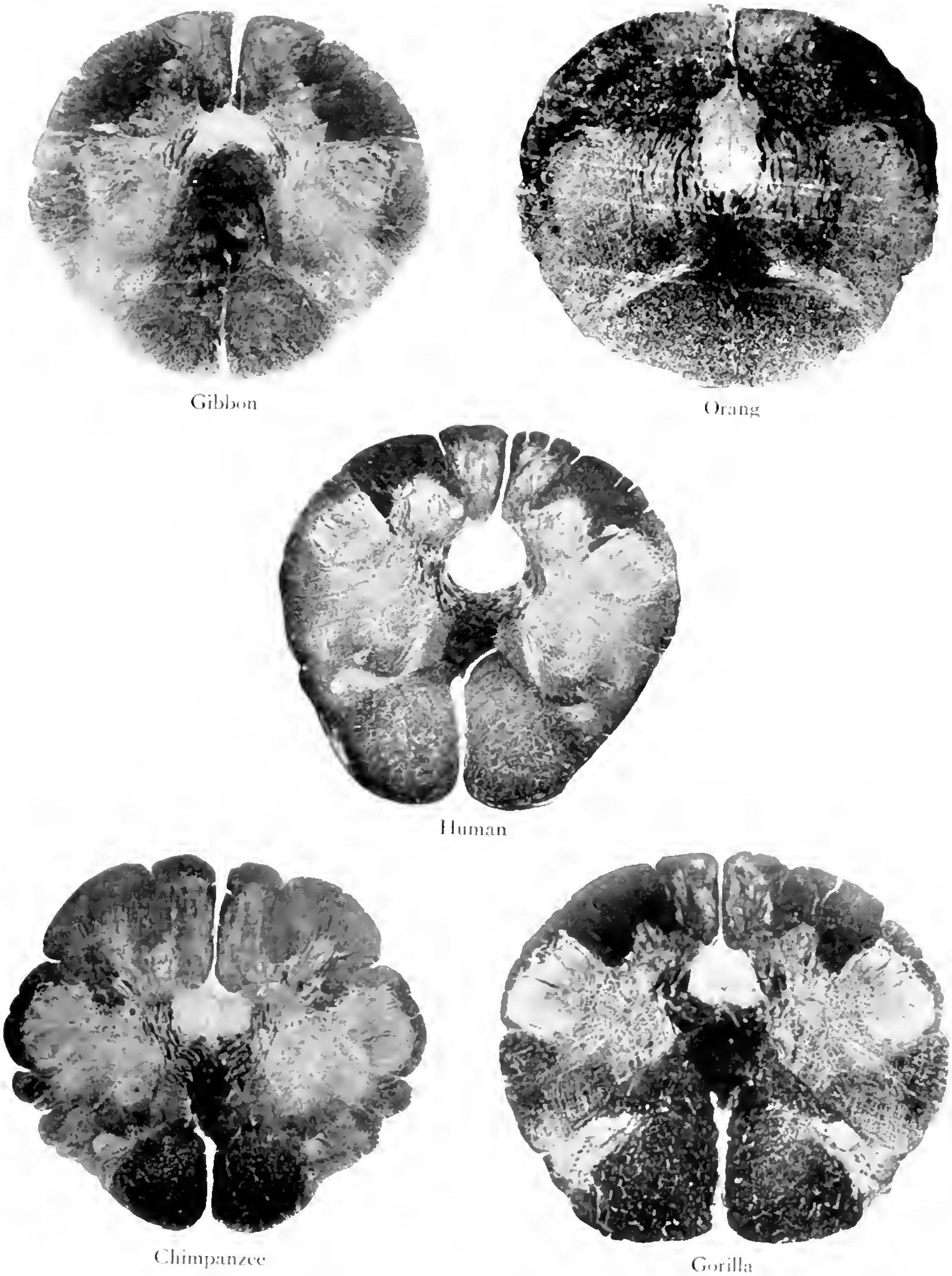
Adaptations in the Vestibular Nuclei. Equally archaic are those centers which receive impulses from the proprioceptors of the semicircular canals, utricle and saccule. These vestibular nuclei show certain fluctuations which, however, are entirely proportional to the equilibratory needs of particular species. In those forms requiring a most effective balancing mechanism, the vestibular complex is correspondingly large; while in species less dependent upon this function, there is an apparent falling off in the general dimensions of the vestibular area. In the main, the receiving stations for this function maintain a minimal standard which is essentially constant throughout the entire order.

It is also interesting to note that tarsius and mycetes (the South American howling monkey) stand at the head of the list as having the highest coefficients in the vestibular complex. This superiority in the balancing mechanism is unquestionably due to the animal's high degree of specialization. In mycetes it is incident to development of the prehensile tail. By this organ the animal adds to its motor apparatus an equipment which permits of suspension in midair and thus frees the hind- and forelimbs for purposes of defense, offense, gathering of food and other activities in which the hands and feet may be simultaneously employed. A species thus specialized would acquire a more extensive functional power of balancing than animals whose base of support and mode of locomotion are less precarious. In other species, the dimensional differences of the central balancing mechanism are almost negligible. At first glance it seems inconsistent that the equilibratory functions of the arboreal animal, which moves about upon such uncertain support as the branches of trees, should not be greater than that of a ground-living form, such as man. Yet there are undoubtedly equalizing factors which serve to offset any tendency toward marked disparity. In the larger anthropoids, for example, the attempt to assume the erect posture and to depart from an arboreal mode of living introduces new equilibratory factors. This specialization reaches its highest degree of differentiation in man, who, while no longer in need of balancing functions adapted to the conditions of arboreal life, has added to his equilibratory responsibilities by developing a type of locomotion in which he must support his body on two feet instead of four. The expansion in the human balancing mechanism, although not incident to tree-climbing or tree-dwelling, is, none the less, a direct response to the factors introduced by bipedal equilibration. Thus, while the archaic structures, representing the balancing mechanism and known collectively as the vestibular complex, show certain limited variations as more definite terrestrial life is assumed, they, in general, maintain a fundamental equality in their coefficient expression. Their variations, however limited, all manifest the effects of adaptive influences and are significant in the sense that they disclose the evolutionary predisposition of neural structures to adjust themselves to varying demands of functional specialization.



FIGS. 471 TO 481. CROSS SECTION AT THE LEVEL OF THE CAUDAL

These comparisons are intended to disclose the internal configuration of corresponding levels in the neuraxis. each level in the several species.



EXTREMITY OF INFERIOR OLIVE IN THE COMPARATIVE PRIMATE SERIES.

They disregard the actual dimensions of the sections. Such measurements are given in the descriptions of

EVOLUTIONAL MODIFICATIONS IN THE DORSAL SENSORY FIELD

Another series of structures represents the centers for myo-articular proprioceptive impulses from the extremities and head. These comprise the nuclei of the dorsal sensory field, including the nucleus of Goll, of Burdach and of Rolando. In their coefficient expressions these sensory elements maintain a fairly constant equality throughout the primate order. There are certain fluctuations in their total representation which depend upon extreme developments, such, for example, as the prehensile tail. It is claimed that this organ, in many instances, serves as a fifth hand. This is true in most of the South American monkeys whose specialization in this respect has been described in Mycetes seniculus.

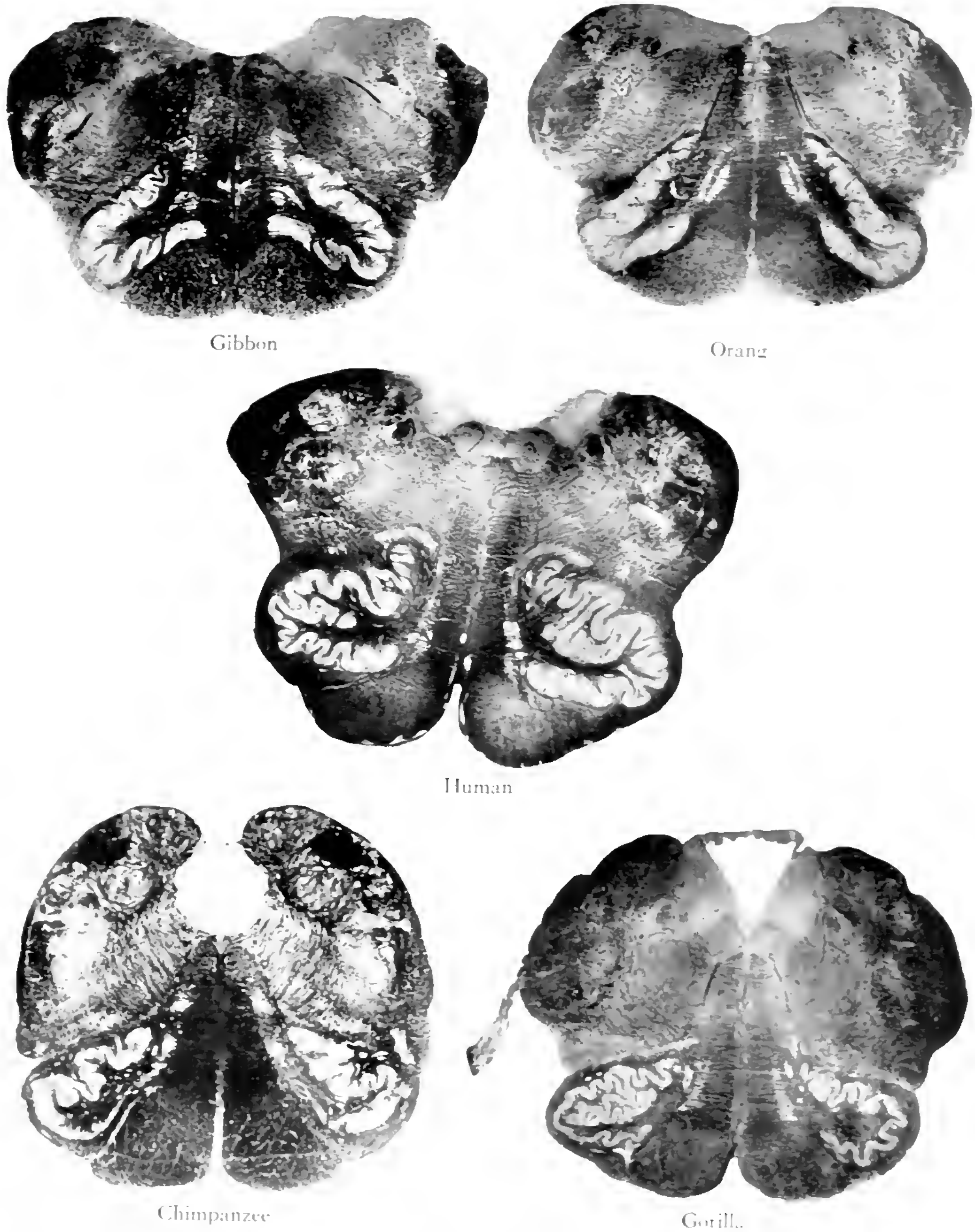
More important than the total volumetric representation of the dorsal sensory nuclei are those relations between them which indicate variations in the differentiation of the extremities. The column and nucleus of Goll representing the lower extremity, foot and tail, when compared with the column of Burdach and its nucleus, the oblongatal representatives of the upper extremity and hand, show a progressive diminution in volume in passing from the lowest to the highest primate. This transitional disproportion from a status in which the clava (column and nucleus of Goll) is distinctly larger than the cuneus (column and nucleus of Burdach) to a condition completely reversing this relation in which the cuneus is at least twice the size of the clava, advances by gradient stages.

The two sensory elements are about equal in Macacus rhesus and gorilla, but in gibbon, orang and chimpanzee, the balance begins to turn in favor of the cuneus. This relation between the two great elements of the dorsal sensory field indicates the evolutional process which has eventually resulted in the production of a bimanal type, capable of the erect posture and bipedal locomotion. Such specialization evolved out of a common and more generalized stock whose inherent tendencies were not only quadrumanal but were further conditioned by the addition of a tail which augmented the stream of afferent impulses from the caudal portions of the body. Gradually the tail became recessive, lost its prehensile or balancing function, and finally disappeared. During this process the lower extremities, and particularly the feet, differentiated for the purpose of supporting the body in the upright position. It was, however, the progressive adaptive development in the upper extremity which gave final preeminence to the cuneus because this structure represented the proprioceptive influx arising from the most efficient organ of construction and analysis yet developed by the vertebrate kind, the human hand.

The relative proportions of the third element of the dorsal sensory field, the nucleus of Rolando, are also significant. It is interesting to note that this nucleus has diminished in all of the primates as compared with the lower mammalian types, such as carnivores or ungulates. To some extent a similar diminution may be observed in contrasting the lower primate forms with those standing nearer to the upper extremity of the order. The decrease, however, is not so impressive as to constitute one of the outstanding features in the transitional changes incident to evolutional adaptation. Such change as does appear depends upon the fact that the face and head have progressively become less important as specialized areas for guiding the course of locomotion. Their offices have largely been superseded by the pronounced development of the hand which has taken upon itself many responsibilities as the chief explorer in the environment, at least in those circumstances demanding actual contact with objects. When compared with the progressively expanding cuneus, the nucleus of Rolando, together with the descending trigeminal tract, stands out all the more conspicuously because it has not kept pace with the expansion which has so strikingly affected its immediate neighbor in the dorsal sensory field. For just as the cuneus, which

FIGS. 482 TO 492. CROSS SECTION AT THE LEVEL OF THE MIDDLE

These comparisons disclose the internal configuration of corresponding levels in the neuraxis. They disregard several species.



OF THE INFERIOR OLIVE IN THE COMPARATIVE PRIMATE SERIES.

the actual dimensions of the section. Such measurements are given in the descriptions of each level in the represents the arm and hand, has gradually gained precedence in size and conducting capacity over the clava which represents the leg and foot, so the dorsal representative of manual differentiation gained preeminence over the nucleus of Rolando and its accompanying fibers, the descending trigeminal tract.

EVOLUTIONAL ADVANCES IN NEOKINESIS WITHIN THE PRIMATE ORDER

If these elements of the brain, including cranial nuclei, reticular formation and nuclei of the dorsal sensory field, express much that is inherently archaic, if they retain in large measure the primordial characters of neural organization involved in such essential functions as respiration, cardiac activity and digestion, the control of deglutition and mastication, the mechanism of balancing, the transmission of proprioceptive impulses from the head and extremities and the regulation of the ocular muscles, there are also elements in the brain which are much more responsive to the influences of adaptation. The structure of these elements possesses a plasticity especially sensitive to the evolutional advances which characterize the new sphere of primate activity.

Were it possible to summarize briefly the outstanding transitions through which these animals have made their steady advance, these features might be said to comprise those specific refinements in motor performances which made progressive adaptation possible. They brought to bear upon the externalizing capacity of the animal more complex syntheses of sensory combinations and gave to the execution of muscular action a greater range of flexibility. They provided the incentive for the constructive faculties of the most facile and adaptable portion of the body, the hand, and sublimated in this facility the powers of selection between alternative courses of action. They added the quality of judgment for manual guidance. They imparted to deftness those factors of creative imagination whose culmination is that vast superstructure representing the civilized world with all its rich content created by the industries and efforts of man. Defined in a single term, this new sphere of action has been called *neokinesis*. Its motor possibilities were first revealed by the advent of mammalian forms. They marked the beginning of that long period of evolutional progress which constantly kept in the foreground the developmental potentiality offering the greatest ultimate promise. Simple as is the neokinetic specialization in most of the lower mammals, it may nevertheless be discerned in its incipiency at that stage of organization when the cerebral cortex first began to differentiate a motor zone for voluntary control over the muscles. This motor zone of the cortex acquired connections with the lower segments of the axis through the projection fibers of the pyramidal system, which introduced all of those advantages accruing from progressive expansions in the hemisphere.

Neokinesis and Development of the Hand. A survey of mammals clearly indicates that those orders which have manifested the greatest capacity in developing neokinesis gradually tended to acquire ascendancy. Certain orders among the mammals, not distinguished by their neokinetic development, have passed into habitat zones in which they reveal no constructive preeminence. They have attained only that scant margin of success which secured to them a nominal degree of permanency in their organic differentiation. How true this is may be seen in the history of the carnivores and ungulates, rodents and insectivores, marsupials and monotremes. Equally true is it of the pinniped mammals, which by secondary adaptation have readjusted their somatic and visceral organization to aquatic life. But the branch of the mammalian stem which manifested a real tendency toward manual differentiation furnishes a totally different record in the history of neokinetic expansion. The first impulses toward this manual differentiation developed certain morphological extremes as, for example, quadrumanal specialization, and thus committed the animal to a type of habitat in which both the fore and hind extremities were employed in a locomotor capacity. Yet in all primates the beginning of this manual expansion is clearly discernible. By means of this differentiation they entered upon a new

TABULATION OF PLANIMETRIC COEFFICIENTS

Species	Pontile nuclei	Pyramid	Peduncle	Olive
Man	.550	.183	.321	.226
Gorilla	.480	.161	.187	.186
Chimpanzee	.400	.172	.223	.174
Gibbon	.200	.138	.110	.155
Macacus	.150	.147	.160	.128
Tarsius	.057	.032	.017	.042
Cat	.080	.062	.064	.061
Rabbit	.054	.029	.044	.030
Giraffe	.063	.030	.067	.042
Horse	.064	.027	.079	.036
Kangaroo	.067	.043	.051	.034
Emu	...	...		.023

Comparative planimetric indices of four important structures in the brain stem of vertebrates. These indices show the marked evolutional expansion in all four structures, especially affecting the primates and emphatically demonstrating the effects of arborealism. Three of the structures are exclusively mammalian. The fourth, the inferior olivary nucleus, is rudimentary in the bird and, when present, in all other lower vertebrates.

world and in the organization of their brain plainly reveal that the key to this new realm was already in their possession.

The development of the paw, the hoof, the claw or the swimming paddle condemned its possessor to the restrictive conditions of a greatly limited habitat. It would actually seem, on the other hand, as though the inception of manual differentiation were an invitation to new freedom, an inspiration for the exercise of that latent power of supremacy which awaited only the acquisition of some adequate instrument whereby to express itself.

Even the low organization of the brain in lemur discloses the first signs of the new impulse to expand the neokinetic portion of the central nervous system. The evidence of its brain indicates to what extent the pyramidal system has increased in volume over and above lower mammalian forms. Thus begun in lemur, the process of expansion goes steadily forward from

COMPARATIVE PLANIMETRIC GRAPHS

A. Olive and Pyramid

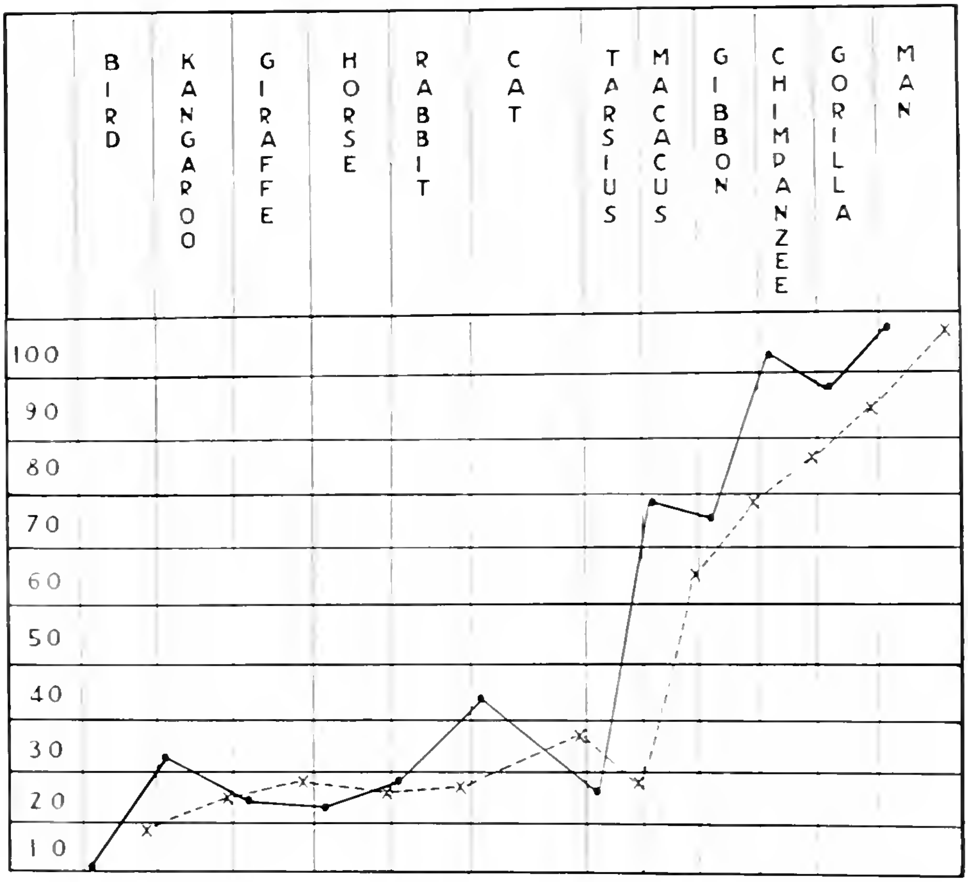
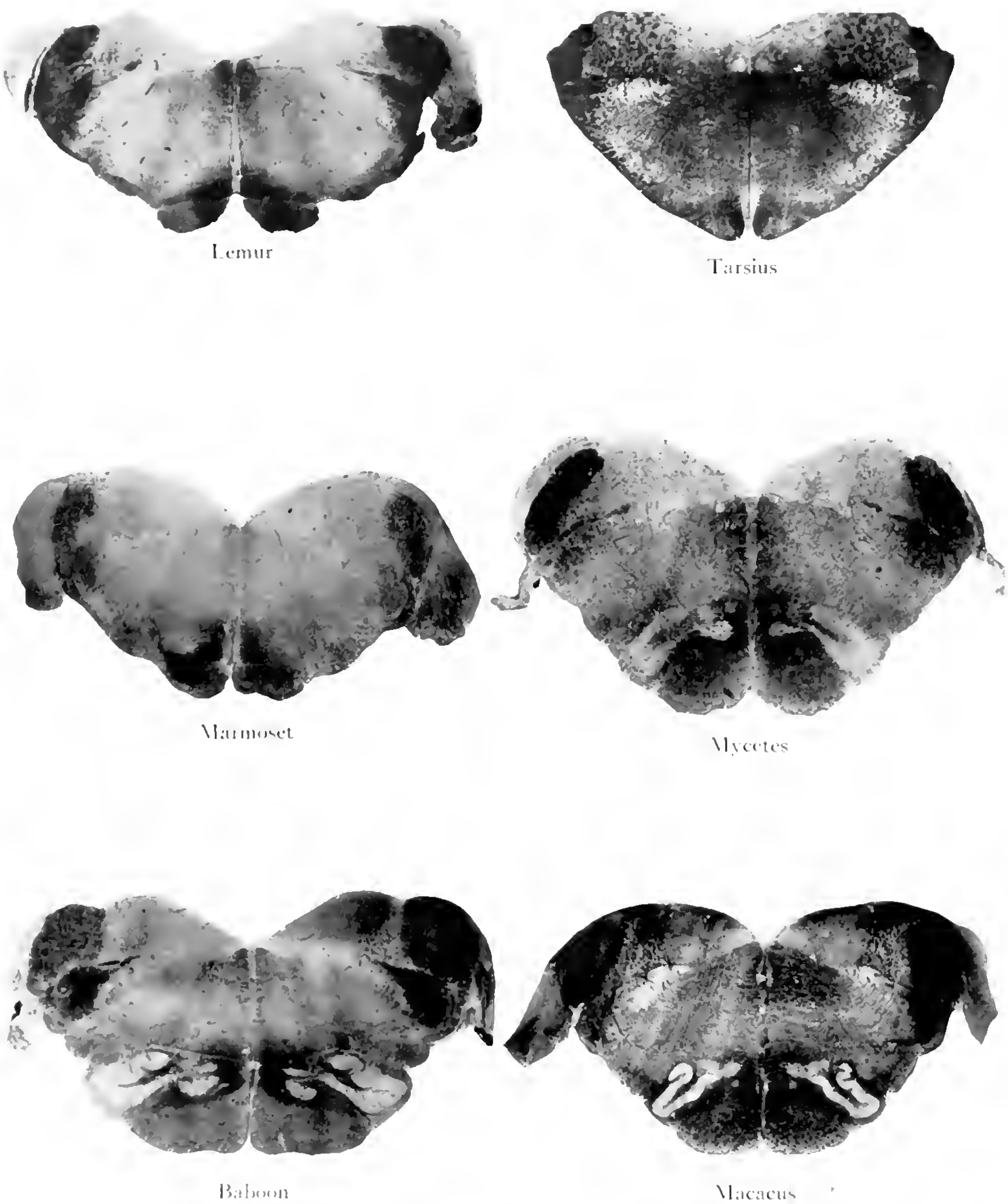


FIG. 403. GRAPHS CONSTRUCTED ON THE BASIS OF THE PLANIMETRIC INDICES.

stage to stage through the primate order until it reaches its highest expression in the human brain. The advance as indicated by increments in the pyramidal system is clearly seen in the lower primates. The marmoset may express this progress somewhat feebly, but the new-world monkeys reassert the growing importance of neokinetic organization. Passing upward to the intermediate primates, the advance is more apparent, with the possible exception of the gibbon in which there appears to be some hesitation. This seeming indecision is due no doubt to the fact that this animal has become largely dependent upon its upper extremities for locomotion and thus has deprived its manual differentiation of a real opportunity to progress. In other words, the gibbon has carried brachiation to an extreme degree.

In the higher anthropoids the upward progress is resumed with unmistakable decisiveness. The orang, the chimpanzee and the gorilla all show marked advance in the pyramidal system which finally reaches its highest proportions in the brain of man. The progressive expansion affecting this neokinetic system represents a characteristic development in the primates. It is graphically demonstrated in tabulations of the planimetric coefficients of the pyramid in which man occupies the highest position, while from him the line descends through measurable gradations to the higher anthropoids, to the intermediate primates, and finally reaches its lowest expression in the tarsier. The difference between the latter and man is approximately fifteen hundredths, which represents a remarkable increment in the volume of the human pyramid. That the difference between these two contrasted forms does not appear more pronounced is due to the fact that the pyramidal tract must accommodate itself to a portion of the neuraxis through which many other equally important conduction systems make their way. The pyramidal system, for example, represents a conduction pathway from the motor or precentral area of the hemisphere. Its axons arise in the giant cells of Betz, leave the cortex, become convergent in the internal capsule and pass through the cerebral peduncle and pons into the medulla oblongata. Each specialized area of the motor cortex, such, for example, as the leg area, contributes axons to the pyramidal tract. According as such motor area of the neopallium is extensively represented, the number of fibers arising in it is correspondingly large or small. The progressive expansion of the precentral area in all of the primates is one of the most noteworthy features in the development of the brain. The motor area itself is activated and guided by neural influences from many other regions of the neopallium. It is, as it were, merely the mouthpiece of the cerebral hemispheres which gives final expression to the neural combinations created within the entire cerebral cortex.

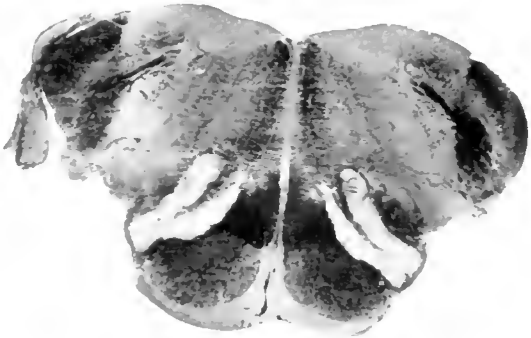
Filling so important an office of transmission, it is apparent that this motor area must be in direct communication with adjacent and more distant portions of the cerebral hemispheres. Such communications may be discerned in the many association fibers, both of the long and short variety, which link the various convolutions together. The important feature concerning the motor area itself is its capacity to sublimate into effective formulas and motor patterns all of that great stream of afferent impulses which enters the brain. These motor patterns determining the externalized expression of the animal's behavior find their ultimate conveyance by way of the pyramidal system. If this system should actually keep pace with the expansions of the cerebral hemisphere by manifesting a corresponding increment in size, it would soon become too extensive for either the brain stem or the spinal cord. That it does not vary directly with the rate of expansion in the cerebral cortex is evident, although cortical expansion does exert a definite influence in increasing the pyramidal volume. It is possible for the cerebral cortex to increase tenfold while the pyramidal system which conveys the impulses for externalizing the activities of the entire neopallium, adds but a small fraction of increment to its size. Thus, the pyramidal tract actually reflects the effort toward condensation which is everywhere imposed upon



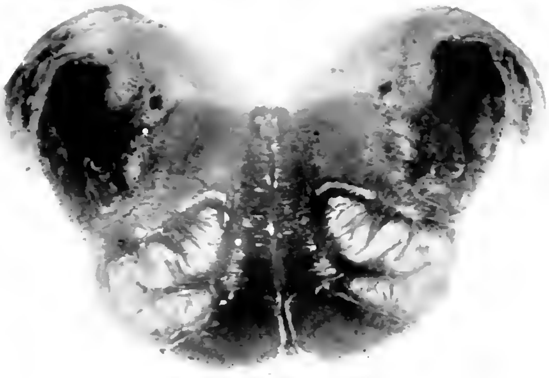
FIGS. 494 TO 504. CROSS SECTION AT THE LEVEL OF

These comparisons disclose the internal configuration of corresponding levels in the neuraxis. They disregard several species.

Gibbon



Orang



Human

Chimpanzee

Gorilla

THE VESTIBULAR NUCLEI IN THE COMPARATIVE PRIMATE SERIES.

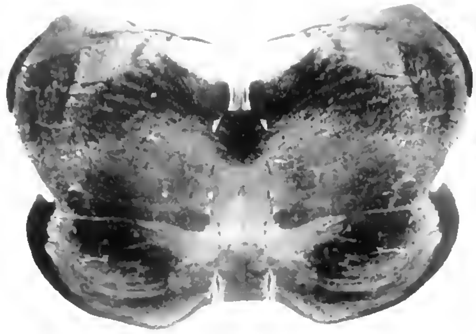
the actual dimensions of the sections. Such measurements are given in the descriptions of each level of the

the neuraxis in the afferent and efferent conduction of impulses over its long projection systems. It is for this reason that even the slightest increase in this system of fibers must be regarded as significant of expansion in the functional capacity which it represents. Upon comparison, the difference between the planimetric coefficients of the pyramid in the marmoset and man is represented only by twelve hundredths increase in favor of the human motor system. Such disparity as this appears relatively small in comparing these two vastly different primates. But when the pyramidal condensation is viewed as the functional representative of large areas of cortex, the pyramid stands out in man in striking contrast to the corresponding system of the lower primates, and manifests the undoubted influences of an evolutional process.

The increase of the pyramidal system, however decisive it may be in its bearing upon the development of the neokinetic functions, is relatively less conspicuous than the expansion of the pons Varolii. This applies most particularly to the pontile nuclei. Two facts show an intimate connection between these nuclei and neokinesis: first, they serve to relay fibers from several areas of the neopallium, and second, the axons arising in them terminate in the lateral lobes of the cerebellum. Interpreted in the light of the function which the pontile nuclei serve, this linking of the cerebral hemispheres with the lateral lobes of the cerebellum is in the interest of the coordinative activities expressed in the appendicular musculature. This conclusion is justified by the fact that experimental and clinico-pathological evidence points to the lateral lobes of the cerebellum as an acquisition of the central nervous system for the distribution of coordinative impulses to the muscles of the extremities. The lateral lobes differ from the vermis since the latter is particularly concerned with the distribution of coordinative impulses to the axial musculature of the trunk, neck and head. From the functional specialization of the neopallial areas participating in the important communication consummated by the pontile nuclei, some conception of their significance may be gained. Many of the pallio-pontile fibers take origin in the parietal lobe, from which region, in fact, they arise in greatest number. This portion of the neopallium is active in the interest of those extensive sensory syntheses essential to general body sensibility. In this broad area of the brain, all of the myoarticular proprioceptive organs have their cortical representation. Here the impulses arising from such receptors become associated as kinesthetic memories and guides for directing all somatic motor activities. Impulses from other types of receptors also find their ultimate area for elaboration in the parietal zone. All varieties of sensory stimuli arising from the exteroceptors contribute to the upbuilding of discriminative sensibility in the parietal lobe. The significance of the parieto-ponto-cerebellar connection in the interest of coordination therefore becomes obvious.

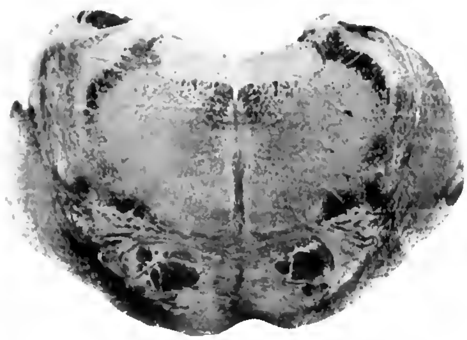
In a similar manner, the large contribution of connecting fibers arising in the temporoparietal region of the brain seems to have its explanation. It is probable that in this territory the neopallium is active in the association of those impulses which arise in the vestibular proprioceptors of the semicircular canals, utricle and saccule. Such impulses are definitely connected with the equilibratory sense and, as such, play an important rôle in the spatial orientation of the body, more particularly of the head. The close connection between the conscious fields of equilibratory sense, of touch and muscle-joint sense on the one hand, and the cerebellum on the other, serves to perfect the coordinative control of muscular activity.

It has long been held that a voluminous bundle of fibers establishes communication between the occipital lobe of the hemisphere and the lateral lobe of the cerebellum. This fact has in recent times been called somewhat in question and the large aggregation of fibers known as the occipito-ponto-cerebellar fasciculus has been ascribed to origins intermediate between the parietal, temporal and occipital regions of the brain. Whether its origin is



Lemur

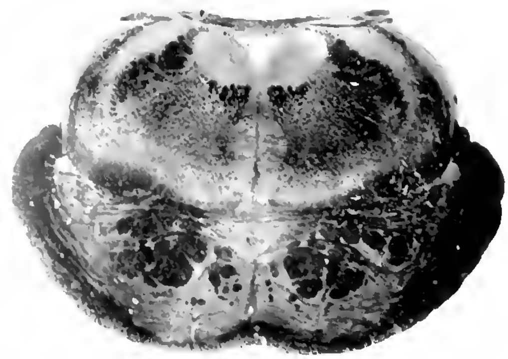
Tarsius



Marmoset

Mycetes

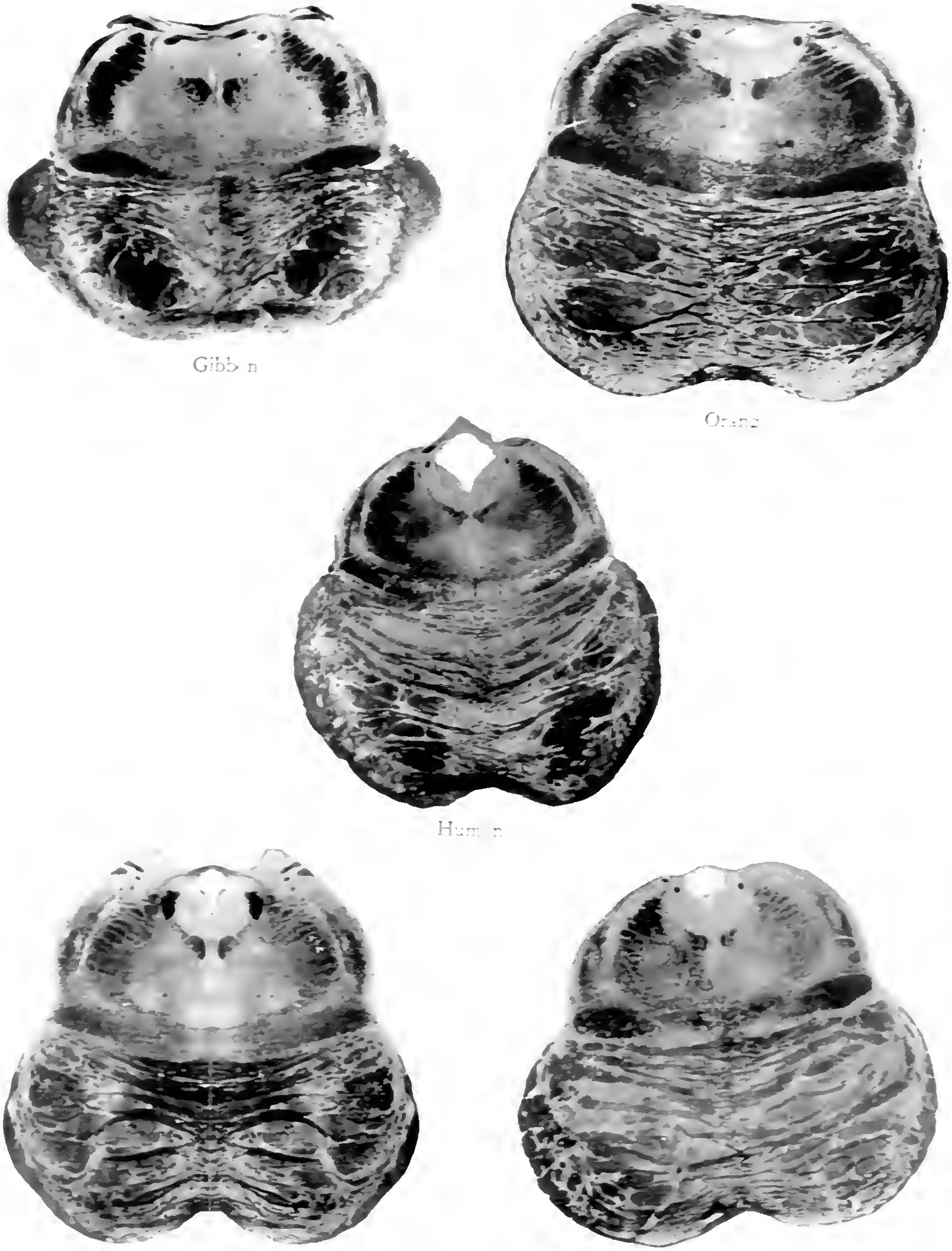
Baboon



Macacus

FIGS. 505 TO 515. CROSS SECTION AT THE LEVEL OF THE EMERGENCE

These comparisons disclose the internal configuration of corresponding levels in the neuraxis. They disregard [illegible]



Gibb n

Oran

Hum n

C m nzee

G

OF THE TROCHLEAR NERVE IN THE COMPARATIVE PRIMATE SERIES.

the actual dimensions of the sections. [illegible] measurements are given in the descriptions [illegible] the [illegible] of the pallio-ponto-cerebellar [illegible]. It [illegible], perhaps, in some common ground in [illegible] of the parietal, of the temporal and of the occipital

COMPARATIVE PLANIMETRIC GRAPHS

B. PONTILE NUCLEI

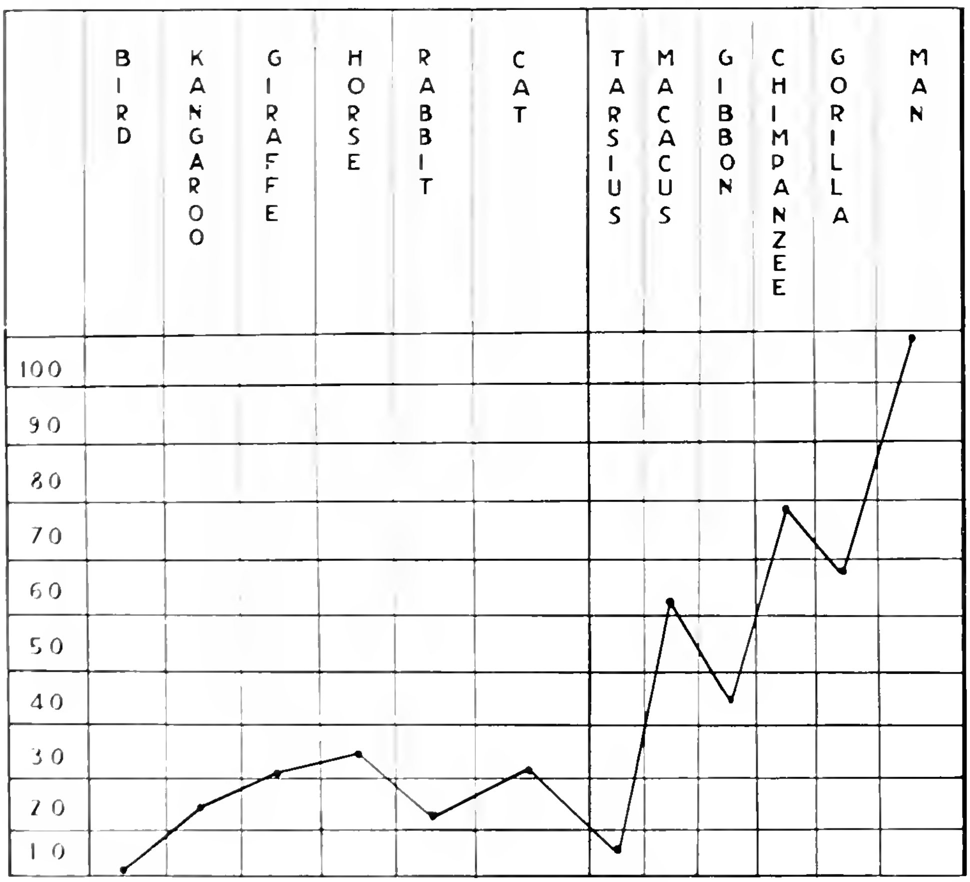


FIG. 516. GRAPH BASED ON PLANIMETRIC INDICES OF THE PONTILE NUCLEI.

[illegible] apparent that the pons Varolii, like other structures in the brain stem [illegible] and rapidly in passing upward through the several horizons of [illegible] of vertebrate organization pontile development is relatively insignifi- [illegible] below the class of mammals. The pons Varolii is essential to the [illegible] organized skilled acts.

cortex approach each other in type of specialization. Such blending of cortical types as this, implicating as it does three discrete areas of the neopallium, might well give rise to a contingent of the pallio-ponto-cerebellar system capable of communicating to the lateral cerebellar lobes impulses which represent a physiological admixture of muscular and equilibratory sensibility with visual-sensory elements. Such a combination of impressions received from the muscles and joints, from the semicircular canals and from the eyes would constitute an invaluable accession in the construction of those neural combinations necessary for the coordinative guidance of movements of the extremities, and more particularly the upper extremity. Whatever function is ultimately ascribed to the occipital contingent of the pallio-ponto-cerebellar system must depend upon future investigation. In general, it may be accepted that this system is connected with the functions of neokinesis, and that its progressive augmentation in the primate series indicates a definite increment in the sphere of neokinetic organization.

The frontal lobe, especially its intermediate precentral area in close relation to the origin of the pyramidal system, also establishes communication with the lateral lobes of the cerebellum through the fronto-ponto-cerebellar contingent. This bundle of fibers is somewhat less in volume than either the occipital or the parieto-temporal contingents of this system. According to present physiological interpretations of cortical localization, the intermediate precentral area has functional control over highly skilled motor performances. The fronto-ponto-cerebellar fibers in this light are not difficult to understand. Both the histogenesis and histology in this region of the human brain furnish excellent reasons to believe that the function of this portion of the cortex is intimately associated with motor activity. Its stratigraphic representation of cells and fibers follows closely the pattern laid down in much clearer outline in the precentral motor convolution.

Those who are opposed to discretely diagrammatic and somewhat dogmatic allocation of specific functions to circumscribed areas of the cerebral cortex may object to this interpretation. Their objections must be received and considered with respect. Nor should they be lost sight of in the further exploration of the cortex. There already exists, however, so much that is convincing with reference to specific localization in the neopallium, that many authorities find no difficulty in attributing to the intermediate precentral area a specific function. Whether or not this function ultimately proves to be the regulation of highly skilled motor performances in no way affects the validity of the large contribution of fibers which the intermediate precentral area makes to the pallio-ponto-cerebellar system. The frontal lobe of the brain is unquestionably connected with the lateral lobes of the cerebellum. Its connection represents some phase in the expression of neokinetic activity. With certain reservations as to the exact significance of some of its constituents, the entire pallio-ponto-cerebellar system may be accepted as an especially reliable index of neokinetic expansion. The relation of the pontile nuclei to this system appears in the fact that they are the relay station for the fibers arising in the several lobes of the neopallium and seeking final distribution in the lateral lobes of the cerebellum. If these nuclei manifest augmentation in passing from the lower to the upper extremity of the order, the inference seems justified that the system with which they are connected has been correspondingly augmented. A progressive expansion of this kind is so prominently demonstrated in the comparison of the primates as to make the pontile nuclei the most significant indicator of the evolutionary process in the brain stem. The planimetric coefficient of these nuclei in the lemur is $5\frac{1}{2}$ hundredths. At the other extremity of the series it is 55 hundredths, a gain of $49\frac{1}{2}$ hundredths in passing from the lemur to man. In no other structure of the brain stem is there such marked expansion. Reconstructions of the pontile nuclei give a still more realistic idea of the progressive increment which they present in this series.

Neokinesis and Development of the Foot in the Assumption of the Erect Posture. While the significance of manual differentiation may be easily appreciated in connection with the progressive extensions in the realm of neokinesis and especially in relation to the expansions of the pontile nuclei, it should not be overlooked that the highest degree of manual adaptability is dependent upon an equally high specialization of the foot. As a matter of fact, the hand in man is less specialized structurally than in many of the apes. It is the extreme specialization of the human foot which imparts to the hand its real functional opportunity to establish manual differentiation as the supreme achievement of neokinetic progress. The apekind, clinging persistently to its quadrumanal type of organization, resisted that decisive influence which began to shape the human foot. Their conservatism was epoch-making. It effectually debarred them from any connection with the human family. It was the parting of the ways which witnessed the beginnings of a new race equipped to stand upright upon two feet and use two free hands in the struggles of life.

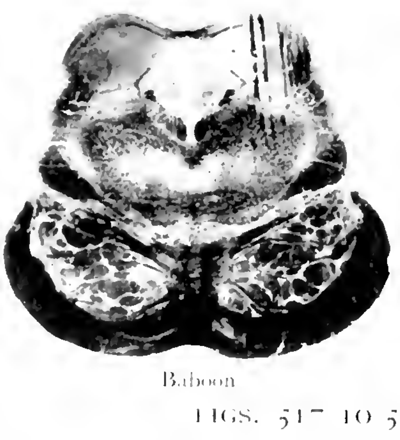
What the pontile nuclei reveal of this process, the cerebral peduncles still further illuminate. The progressive development of the peduncles may be seen almost without aid of mensurational methods. There is, however, marked disparity in volumetric expression between the cerebral peduncle of the marmoset, whose planimetric coefficient has a value of 10 hundredths and that of man, where its value is a little less than 30 hundredths. Between these two extremes are all of the intermediate grades indicating progressive increment. Since the cerebral peduncle comprises all of the fibers arising from the motor area and constituting the pyramidal system, as well as all of the fibers forming the pallio-pontile system, its size accurately reflects the degree of expansion in the cerebral hemisphere.

Lemur

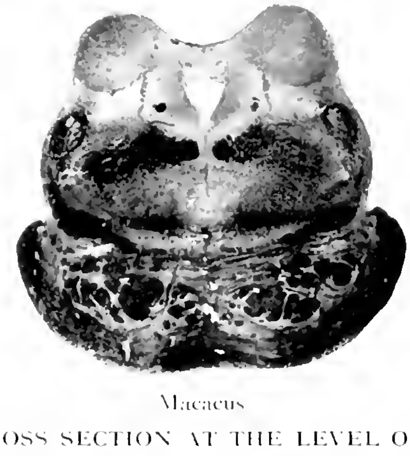
Tarsius

Marmoset

Mycetes



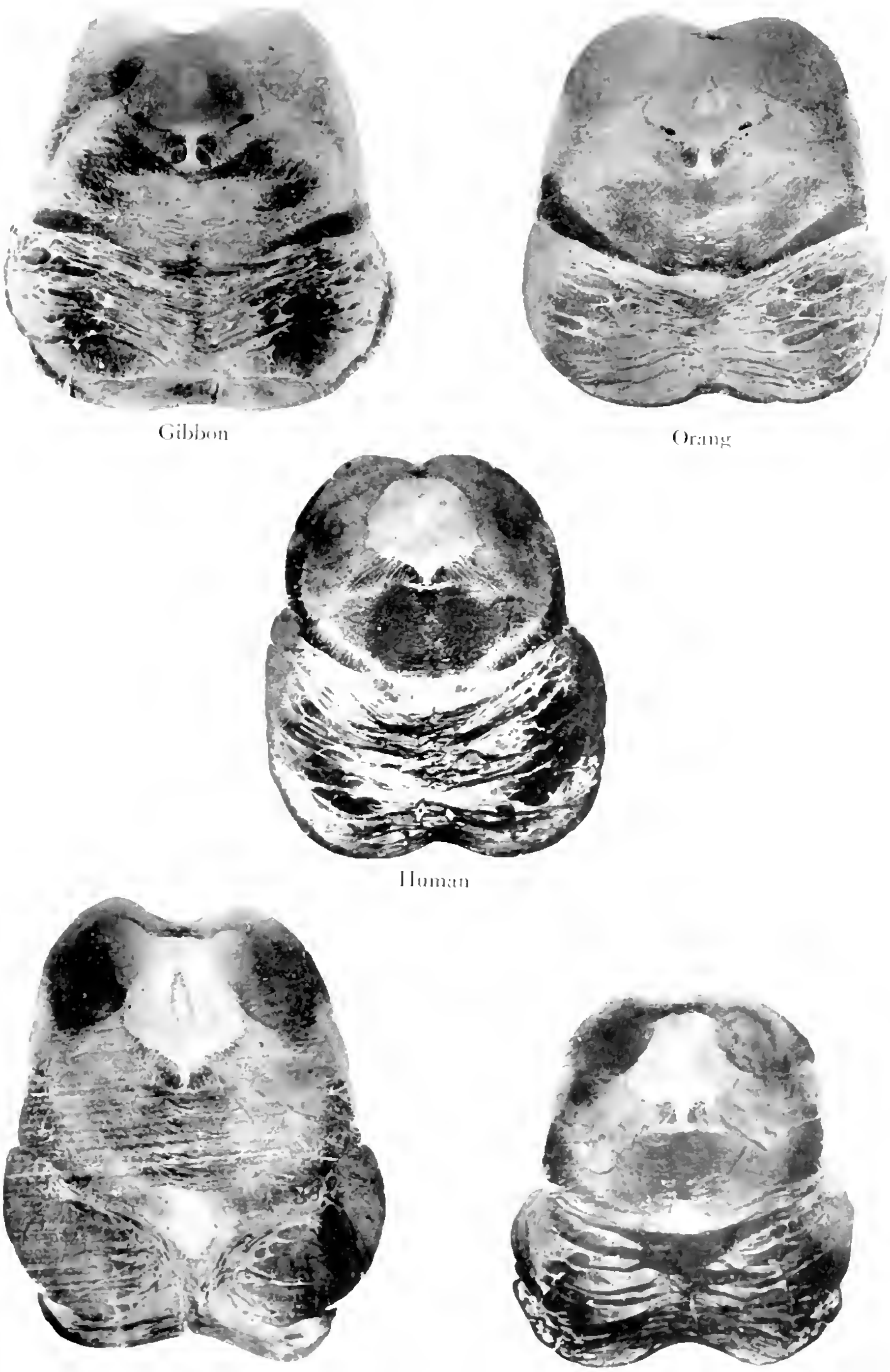
Baboon



Macacus

FIGS. 517 TO 527. CROSS SECTION AT THE LEVEL OF THE

These comparisons disclose the internal configuration of corresponding levels in the neuraxis. They disregard several species.



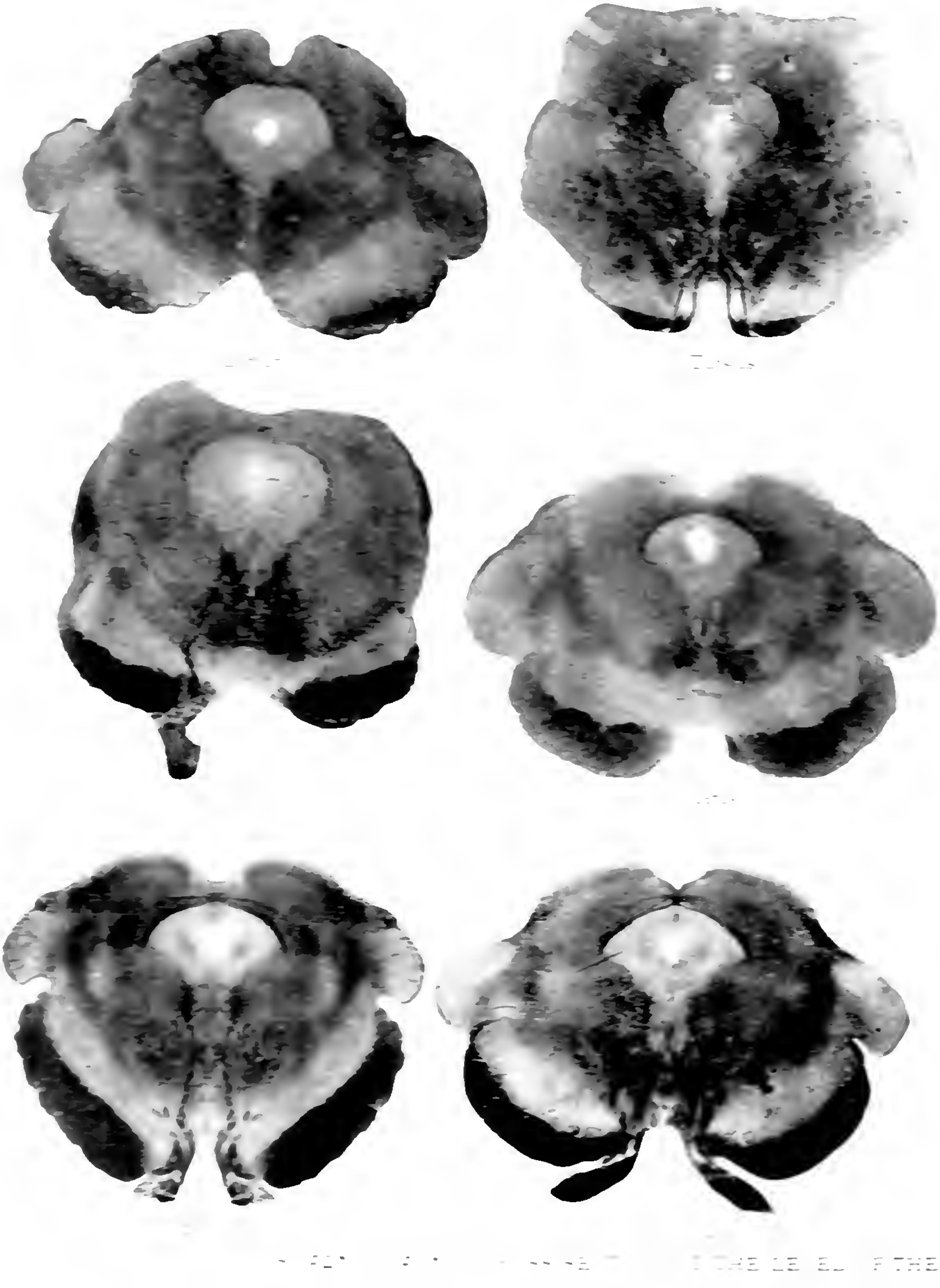
Gibbon — Orang — Human — Chimpanzee — Gorilla

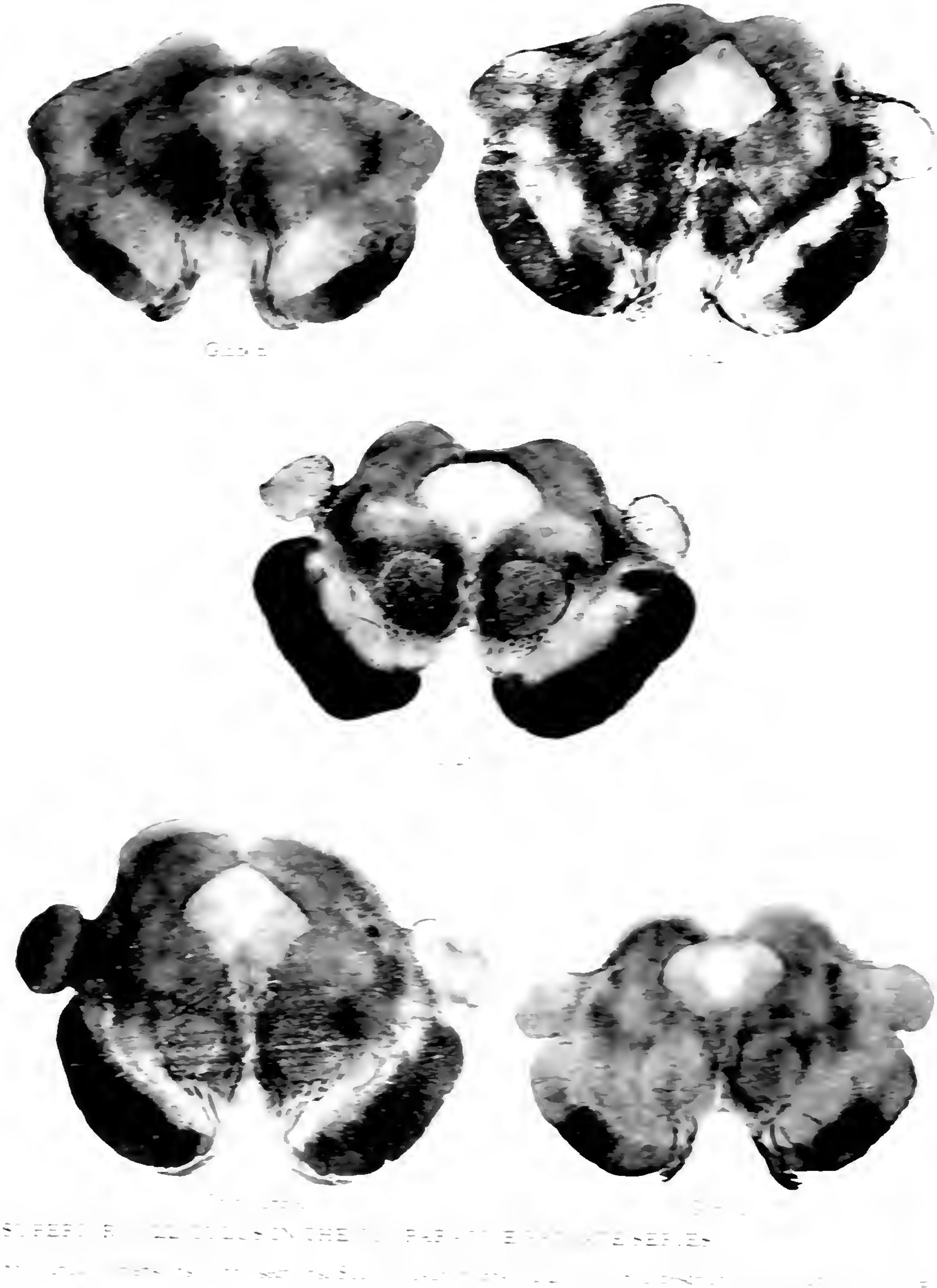
INFERIOR COLLICULUS IN THE COMPARATIVE PRIMATE SERIES.

the actual dimensions of the sections. Such measurements are given in the descriptions of each level of the

A comparative survey of the ventral surface of the brain stem discloses at once progressive extension in the neopallium. The first appearance of the pyramid, the pons Varolii and the cerebral peduncles announces the advent of the mammalian orders and introduces a new epoch of brain development. Along many different lines of activity the mammals have endeavored to make use of their new cerebral endowments. Many different kinds of extremity differentiation have responded to this cerebral specialization in order to develop new means for expressing the potentialities of neokinesis. Hoofs, claws, paws and even paddles in the pinniped carnivores have made their appearance as the agents for externalizing these new capacities of behavior. Each of these in its turn has labored under those inherent disadvantages peculiar to appendicular structures which are wholly dominated by locomotor function. The specificity of locomotor performance in such forms as the kangaroo, the rabbit, the giraffe, the elephant, the horse, the whale or the seal curtailed the opportunities which these animals might possess for the upbuilding of a highly complex sphere of behavioral reaction. To some extent the differentiation of the extremities was of service in utilizing energy in combat and in obtaining food supply. But the motor formulas expressed in locomotor activity, in acts of offense and defense, or in quest of food, with the exception of their distinct increase in the complexity of motor pattern, show little of real advance over such lower vertebrates as the birds and the reptiles. In most of the mammalian orders the impression is unavoidable that all attempts toward developing the sphere of neokinesis, however obviously seeking adequate channels through which to express themselves most effectively, came for the most part to naught, or only advanced to indecisive advantages, until the factors culminating in the primate order made themselves felt in a crucial specialization. The fore- and hindlimbs, designed primarily as locomotor organs, now attained those powers capable at length of throwing off the yoke which subjugated the extremities to the service of locomotion. Thus, the primate brain, through its gains in neokinetic expansion, began to show those real accessions which are sought for in vain throughout all other orders of mammals. Yet the primates were not without their own serious embarrassments. The quadrumanal development so characteristic of all simian tribes gives neither the hand nor the foot its full or ample opportunity for ultimate differentiation. Arboreal life imposed a severe handicap in that it demanded in upper and lower extremity alike a high degree of prehensile specialization for locomotor function. On the other hand, the progressive advance in the neokinetic indices of the brain, especially in the pyramid, the pons Varolii and the cerebral peduncles, discloses the manner in which an exquisite arboreal specialization has been slowly superseded, first by semi-arboreal adaptation, then by imperfectly organized terrestrial life, with the gradual assumption of the erect posture and the almost exclusive adoption of the surface of the earth for transportation. During this process the hand became the supreme agent for externalizing the full expression of these advances.

Other Structures in the Brain Stem Indicating Neokinetic Development in the Primates. The insistence of neokinesis to find adequate expression is again and equally well illustrated by structural extension of certain elements functionally connected with the maintenance of coordination. From the standpoint of volumetric expansion and progressive advance in organic definition, there is no structure in the brain which appears to be more susceptible to the influences of adaptation than the dentate nucleus. Its planimetric coefficient, which in marmoset is 7.7 per cent and in man 17.6 per cent, shows a progressive gain of about 10 hundredths in volume. Even more pronounced is its increasing discreteness as a nuclear structure. With the possible exception of the inferior olivary nucleus, the nucleus dentatus is the most striking example of progressive definition in the entire brain stem. Starting as it does in a diffuse, irregular nuclear aggregation, it passes through many





developmental gradations until it attains its definitely convoluted stage first seen in the gibbon, but steadily increasing its nuclear individuality in the higher anthropoids and man. Not alone does this nucleus acquire decisive

COMPARATIVE PLANIMETRIC GRAPHS

c. CEREBRAL PEDUNCLE

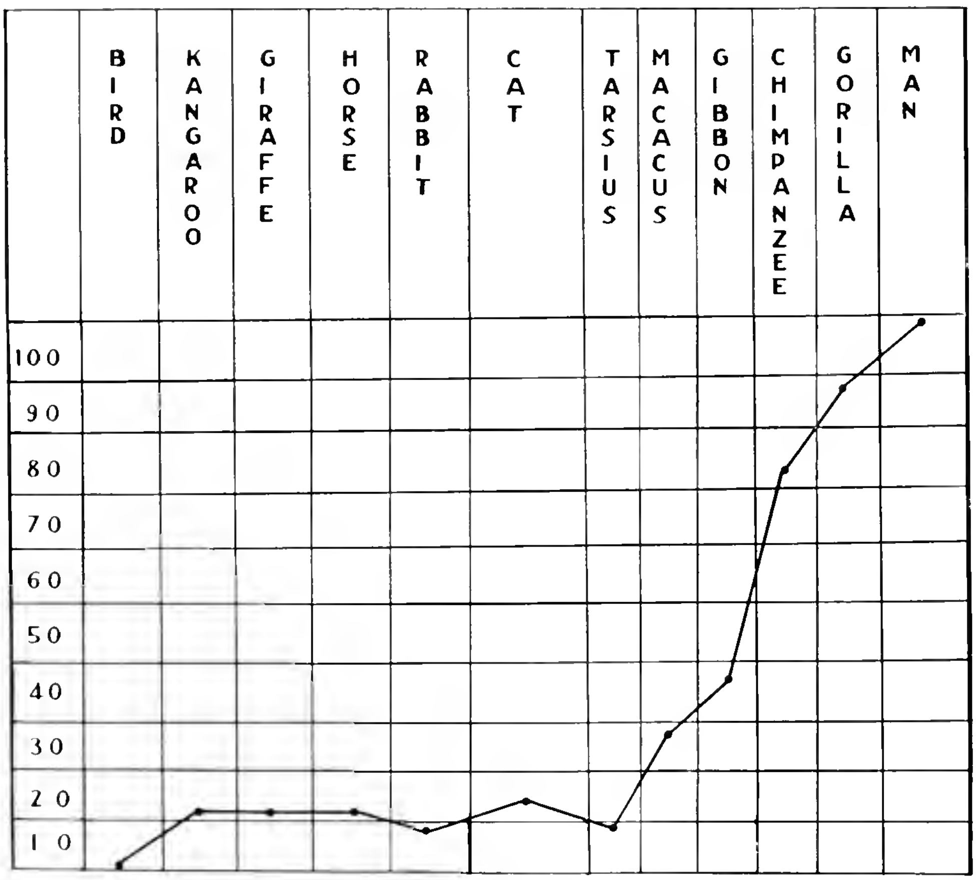


FIG. 539. GRAPH BASED ON PLANIMETRIC INDICES OF CEREBRAL PEDUNCLE.

[illegible] of particular significance in neokinetic evolution. It is a concentrated expression of the [illegible] of the cerebral cortex, representing as it does the palliospinal and palliopontile projection [illegible]. Functionally it provides for the conduction of impulses essential to volitional and coordinated [illegible] muscles. It is of an exclusively mammalian character in the brain, showing its greatest expan- [illegible] influence of arboreal life and the consequent development of quadrumanous specialization.

specialization in the course of its own evolutionary progress; its advances in this respect gain even more emphasis because of their association with the simultaneous increase in size of the lateral cerebellar lobes. These lobes, as well as the dentate nucleus, expand in direct proportion as manual differentiation becomes more definitive.

In a similar manner, the red nucleus, serving as the intermediate relay for impulses from the cerebellum, affords an index of the coordinative capacity of the lateral cerebellar lobes. Attention has already been called to the probable dual nature of the red nucleus as a relaying station. That it serves other offices than the conduction of coordinative control seems likely. On the other hand, the concomitant expansion of the dentate and red nuclei in passing from the lowest to the highest of the primates speaks strongly in favor of its relation to the impulses essential to coordinative control of the upper and lower extremities. The red nucleus does not itself disclose any specific participation in the neokinetic advances of the upper extremity. Its close incorporation in the cerebellar mechanism, however, makes it probable that it receives its chief incentive toward expansion from the accession of coordinative impulses essential to control the muscles in the upper extremity. The difference in the planimetric coefficients of the red nucleus between the lowest of the primates and man is a little over 10 hundredths. In this respect it coincides closely with the similar difference existing between the dentate nucleus at the two extremities of the order.

The volumetric comparison of the superior cerebellar peduncle which connects the dentate with the red nucleus corroborates the conclusions concerning the progressive increment in coordinative control. This structure also shows a progressive augmentation in passing from the lower end of the series to its upper extremity. The significance of all of these elements related to the cerebellum bears definitely upon the field of neokinesis inasmuch as they are all alike involved in the coordinative control of the appendicular musculature.

In its progressive expansion, the inferior olivary nucleus is a distinctive feature in the brain. Concerning the actual function of this important structure, much light is still needed. The interpretation advanced in this discussion of the primates, assigns to the nucleus an activity related to the simultaneous coordination of the hand, head and eye. Integration of widely separated muscles so that they act as a single mechanism needs no argument to defend its physiological necessity in the interest of highly organized motor performances. A vast range of skilled acts depends upon the harmonious action of the eye muscles in order to keep the objective in clear vision and focus. The hands which perform the actual execution of the movements are followed and directed by vision. The underlying motive for the simultaneous cooperation in the muscles turning the eyes, turning the head, as well as moving the hands and fingers, is thus obvious. Ocular supervision is essential both in the acquisition and the direction of a large number of skilled learned performances. From the known facts concerning the inferior olive, this nucleus stands as an intermediary between the ocular nuclei, lying above it in the brain stem, and the nuclear centers forming the final common pathway for motor impulses to the muscles of the neck and the upper extremities. Equipped to receive proprioceptive impulses from the musculature of the eyeball, of the neck and of the upper extremity, the inferior olive is in a position to transmit these incoming impressions to the cerebellum, not only to its lateral lobes, but to some extent also to the vermis. It supplies in this manner the afferent elements to the cerebellum necessary for the organization of outgoing syntheses of coordinative impulses for all highly skilled acts of the body. This is the control essential in the oculo-cephalo-gyric movements utilized in the visual direction of many acts, such as handwriting, painting, drawing and the employment of instruments and implements.

Fundamentally the inferior olive is an ancient structure. Those who have given attention to its phyletic organization recognize in it at least two parts,

i. e., the paleo-olive and the neo-olive. In the lower forms of animals not yet possessed of anything approaching manual differentiation, the need of an intimate cooperation between muscles of the eyes, of the neck and of the upper extremity is not pronounced. These animals in consequence depend upon the associations of a much simpler range of motion. To them the coordination of the neck muscles controlling the movements of the head, and of the eye muscles regulating the movements of the eyeballs, may be essential in such acts as browsing or grazing, particularly to animals possessing long necks, such as the giraffes. These species are not in need of simultaneous coordination in the ocular, cervical and brachial muscles. In consequence, although they have developed an inferior olivary nucleus, this structure appears in its simplest form. It consists largely of what is properly called the paleo-olive. The paleo-olivary connections with the cerebellum are for the most part with the central portion or vermis. In animals possessing claws, such as those of the canine and feline families, there is at least some slight demand for coordinative action between the muscles of the eye, neck and upper extremities. In such species the inferior olivary nucleus shows considerable advance notwithstanding the fact that it still remains, from a structural standpoint, in a fairly primitive condition. Canine and feline activities in which the claws are employed, as in digging holes for burying food, require a certain degree of mutual coordination in oculo-cephalo-gyric and upper extremity movements. These movements unquestionably belong to the category of performances learned by imitation. In consequence there is some increase in these animals of the inferior olive and the olivo-cerebellar connections.

With the advent of the primates, manual differentiation became a feature of progressive development. The influence of this new impulse was immediately impressed upon the inferior olivary body. Even in the lemurs, the nucleus manifests tendencies toward expansion in its neo-olivary portion whose further progress imparts such prominence to the evolutionary process in the primate brain. Thenceforth, throughout the order, this impulse toward neo-olivary expansion becomes more pronounced. When, however, the demands of neokinesis called for greater functional activities in the sphere of olivary action, no distinctly new element was added to the structure. Phyletically ancient portions were so extended as to create, out of the old, new and needed material for amplified functional capacity. This is the underlying principle which in the main characterizes the modifications in the vertebrate brain. The structural substratum of expansion usually exists in rudimentary form awaiting only the demand and opportunity for further development. The inferior olivary body, illustrating this principle, expands in response to increasing demands for functional control in its sphere of action. As evidence of an evolutionary unfolding, it is second to no other element in the entire brain stem. The planimetric coefficients of the olivary nucleus in primates indicate that in passing from its lowest organization to that representative of man, there is a total gain of almost 20 hundredths. In the marmoset the planimetric coefficient of the inferior olive is 3.8 per cent, while in man it is 22.6 per cent. A volumetric gain of such proportions cannot possibly be without great biological significance. More conspicuous even than this increment in volume is the increase in the olive's morphological individuality and definition. With this progressive olivary specialization, the connection of the nucleus with the lateral lobes of the cerebellum becomes more extensive. This fact strongly suggests that the biological impulse underlying this olivary differentiation is closely related to those causes which activated the expansion of the lateral cerebellar lobes. It is well established that the extensions in the lateral portions of the cerebellum have been induced by the progressive specializations in the extremities, more particularly in the upper extremity and hand. The inference seems justified, therefore, that the olive itself has also responded to this same incentive.

Like the lateral lobes of the cerebellum, it must be functionally associated with the developments of neokinetic progress. The inferior olivary nucleus thus corroborates the evidence supplied by the pyramid, the pontile nuclei, the cerebral peduncles, the dentate nucleus, the red nucleus and the superior cerebellar peduncle. All of these parts of the brain, by reason of their expansion, stand out as prominent signals of evolutionary advance.

Certain constituents with equal force denote this process, not by expansion but by progressive diminution in size. Among these structures the most prominent are the superior and the inferior colliculi of the midbrain. Their importance in relation to the special senses of hearing and of sight has been emphasized. The deflorescence in the inferior colliculus is particularly striking showing, as it does, a decrease in planimetric coefficients between lemur and man of over 13 hundredths. While in the case of the superior colliculus the decrease in structural prominence is not so pronounced, it is nevertheless clearly evident that a progressive decline proceeds through all of the primate species from lemur to man, with a total decrease of something more than 4 hundredths.

That the mesencephalic colliculi are remnants of prominent features in lower vertebrates, and that they still retain in these classes a predominance in encephalic organization, has been frequently reiterated. This is the condition in birds, reptiles, amphibians and fish, but with the appearance of the mammals, the introduction of the neopallium concentrated the full force of development upon the hemispheres. In consequence, this part of the brain soon gained preeminence which in large measure was due to the unremitting attempts to capitalize still further the new endowments of neokinetic behavior. Each of the special senses, with the exception of the olfactory sense, participated in these attempts. These senses sought an advantage in proximity to each other which representation in the cerebral cortex afforded them together with more ample opportunities for functional expansion. The optic lobe of the midbrain, compared with the more cosmopolitan advantages of the cerebral cortex, became an environment too provincial and limited for the ultimate development of vision. The sense of hearing was similarly affected in its disposition toward its original mesencephalic allocation, once the neopallium had revealed its developmental possibilities. Hearing followed the example of vision and together they sought new fields for expansion in the hemispheres of the endbrain.

The delegation of auditory and visual function from the roof of the mesencephalon to areas in the cerebral cortex is part of that process of telencephalization which has progressed through the mammalian orders. Its obvious purpose was to procure for these special senses more expansible areas for their elaboration with other types of sensibility. As in all other instances, the prime object of such expansion was not merely the extension of the special sense involved, but much rather the multiplication of its capacities for expression. Thus, increasing the spheres of vision and of hearing had far-reaching effects upon the expansion of neokinesis. The functional increments to the sense of hearing, in consequence of its neopallial opportunities may be clearly witnessed in the expression of articulate speech. To many other human activities hearing has become essential. The auditory development that leads to the recognition and combination of sounds in the form of music and the ultimate externalization of such auditory syntheses in the musical productions of the voice or by manipulation of musical instruments reveal the important rôle which the sense of hearing plays in the extension of neokinetic achievements. Its instrumentality in the processes of learning is obvious, for without such auditory assistance it is probable that many of the highly skilled performances of which man is capable would fail of their complete development and lack one of the chief stimuli which incite, create and direct them.

In similar manner, the expansion of visual function which has taken place in the progressive augmentation of the occipital lobe makes its contribution to the organization and advancement of neokinesis. A large proportion of all skilled motor performances in man depend primarily upon vision for their acquisition. They are equally dependent upon visual integrity for their execution. This applies particularly to the minute and precise skilled acts of the hand involved in writing, in drawing, in painting, in sculpture. It must be apparent, therefore, that the purpose of providing vision and hearing with their ultimate opportunities for expansion in the cerebral cortex is especially concerned in the influence which they exert upon the development and maintenance of neokinetic activities.

In passing from the lower primates to man, the progressive development of the oculomotor decussation is so striking as to leave no doubt concerning its evolutional significance. As interpreted in this discussion, it makes provision for the most complete conjugate association of the eyes. The absence of such internuclear connection would scarcely permit of that intimate cooperation between the movements of the eyeballs essential to holding the visual axes in parallel or producing those degrees of convergence necessary to stereoscopic vision. In other words, without this connection the appreciation of objects and their spatial relations, more particularly in the near ranges of vision, would be incomplete and the more exact application of finer manual movements would thus be greatly curtailed. How essential such stereoscopic vision is to the skilled acts of chirography, painting and sculpture scarcely needs more than mention to establish its claim. From this viewpoint it is again evident that the specific purposes of neokinesis have been served by the development of the internuclear connections of the oculomotor nerves. By mensuration the disparity between the lemur and man, in the oculomotor decussation, is the most pronounced of all figures quoted. Lemur has a representation in its longitudinal coefficient of 16 per cent, while in man this figure rises to the value of 90 per cent, a total difference of 74 hundredths between the two extremities of this order. From such a difference in values, it may be inferred that the functional importance of stereoscopic vision has increased most particularly in proportion to the degree of application of the hand in the execution of the most highly organized motor performances.

The motive running through this entire process of development is not difficult to appreciate. Some parts of the brain, essentially progressive in their tendencies, have reacted by what seems to be an almost enthusiastic response. They have grown in their proportions and gained preeminence in their influence. This is especially true of the neopallium, of the pyramid and pons, of the cerebral peduncle, of the lateral lobes of the cerebellum and the structures connected with them. Some parts of the brain have manifested greater conservatism in their adaptive reactions, as, for example, the centers of the balancing mechanism, or those for the transmission of other proprioceptive impulses. Still other parts, like most of the cranial nerve nuclei, have been actually resistive in their greater phyletic stability, although even they have not escaped the progressive influences arising from such advanced acquisitions as the development of articulate speech, of emotional expression and of stereoscopic vision.

A complete tabulation of the planimetric coefficients for all of the structures which have been discussed in their evolutional relations is appended on page 1037. The coefficients have been so arranged as to give them their sequential order of importance with reference to the evolutional process which they individually represent. It will be observed that they fall naturally into three groups—those preeminently concerned with the expansion in the neokinetic sphere, those to some extent intimately connected with this expansion and those representing archaic structures which have felt in a much more remote manner the influences of neokinetic development.

PLANIMETRIC COEFFICIENTS OF THE PRIMATE BRAIN

	Man	Gorilla	Chim-panzee	Orang	Gib-bon	Ba-boon	Maca-cus	My-cetes	Marmo-set	Lemur	Tarsius
Pyramid	183	161	172	160	138	143	147	137	064	110	032
Pontile nuclei.	550	480	400	300	200	164	150	103	095	055	057
Cerebral peduncle	321	187	223	110	110	190	169	144	079	086	017
Inferior olive	226	186	174	172	155	125	128	120	038	060	042
Nucleus dentatus	176	152	136	160	134	165	155	130	077	110	.059
Nucleus globosus	023	0095	018	015	020	023	014	032	050	032	037
Red nucleus	128	096	086	087	051	060	.057	081	044	012	034
Superior cerebellar peduncle	088	047	047	.064	063	044	046	036	048	033	032
Inferior colliculus	070	111	132	131	130	155	175	.182	210	223	337
Superior colliculus	104	140	125	124	132	173	158	.161	.154	140	230
Nucleus of Goll	064	086	050	048	034	086	076	131	068	041	026
Nucleus of Burdach	100	081	073	093	068	065	086	113	043	049	029
Nucleus of Deiters.	065	072	077	054	085	060	075	114	077	082	180
Nucleus of Schwalbe.	075	070	080	055	092	095	087	090	060	045	062

SUMMARY OF THE EVIDENCE OF AN EVOLUTIONAL PROCESS AFFORDED BY THE EXTERNAL AND INTERNAL APPEARANCE OF THE PRIMATE BRAIN

In sum total, the evidence afforded by the external appearance of the brain in primates, and by its internal structure, points conclusively to an evolutional process which has run parallel with corresponding expansions in behavioral development. This evolutional process, both in structure and in function, has made itself apparent most particularly in the accessions to the sphere of *neokinesis*, which new type of motor expression has been the distinguishing contribution of the mammals. It was, in this respect, as though their arrival had at once opened a new trail which led into realms of more highly specialized behavioral development.

NEOKINESIS AND PALEOKINESIS. This new motor specialization introduced by the mammals had certain advantages over the ancient type peculiar to phyletically more primitive animals, such as birds, reptiles and fish, which, because of its very primitiveness, is known as *paleokinesis*. These two types of motor organization, the new and the old, differ from each other in certain decisive characteristics. Perhaps the one most essential difference between them appears in the insertion of an appreciable period of latency between the receipt of the afferent stimuli and the production of the corresponding motor response. This period of latency has resulted in retarding the immediacy of reflex action. In that interval thus created between the receipt of the afferent stimulus and the dispatch of the efferent impulse, provision is made for more effective sensory associations, more complex combinations of neural impulses activated by the approach of the afferent stimulus. It also provides for such important conditioning qualities of motor response as reflection, selection and the introduction of the influences of previous experience as well as the advantages of higher intelligence. Such a period of latency has in it all of the possibilities of withholding action for relatively long intervals of time, and thus conferring the far-reaching benefits of that important neural attribute known as *inhibition*. The real advances of behavior for which this new element of motor organization lays the foundation become obvious at once. For the direct reflex reaction, it substitutes the deliberately considered act. For the limited reflex motor pattern, it substitutes the more complexly organized motor design. In general, primitive paleokinetic activity is in its nature much more immediately reflex and has but little reflective character. It makes the most advantageous use of automatic and routine precisions in motion, but, on the other hand, permits of little or no variation in its reaction patterns. Neither does it allow of much reconditioning by new influences and elements. It is exquisitely objective in its execution which appears to be as rigidly prescribed as it is invariable in production. It possesses all of the characteristics necessary for generic adaptation and but few of those qualities essential for individualized adjustments. In contrast to it, the more recent mammalian acquisition of neokinesis, by adding the advantages of reflection and deliberation, makes motor reaction more flexible and behavior more widely adaptable. The period of reflection and latency permits of better guidance of movement by the direction of vision, of hearing and of proprioceptive organization. It likewise affords all of those opportunities essential to extensive teachability.

Extent to Which Mammals Utilized Their New Possession of Neokinesis. Although the mammals from their beginnings came into possession of this great advantage over the more lowly organized vertebrates, they did not in all instances utilize it to its full extent. Nor did it become a *sine qua non* guaranteeing a full and effective development of its potentialities in all cases. Indeed, it seems much more as though the mammals were continually striving to find that path which might profit them most in the development of their new possession. But for all their efforts, they were surprisingly unsuccessful in arriving at the desired goal. How they began to push forward along this line in their early monotreme beginnings, how far short they fell of any real progressive achievement, how they tried again and again, now in marsupial specialization, now as rodents, insectivores, bats, ungulates, cetaceans or carnivores, but always without approaching nearer to the desired end, is revealed by their several histories. That they had made definite contributions over and above the lower forms of vertebrates in the organization of motion and in the development of behavior is not difficult to establish. Yet each ordinal specialization, with all its striving in this direction, seemed deficient in some essential equipment whereby it might fulfil the promise discernible in the new accession to their development. Their motor adjustments were largely adapted for transportation, for carrying the body over the surface of the earth, under the earth, in the water or through the air. These animals progressed but little in their constructive processes as applied to their environment. They accepted the earth as they found it and left little behind to change its appearance as a result of their own efforts. Their expansions in neokinesis, like their developments in behavior, were strictly limited by the handicaps of highly restrictive specializations in their instruments of externalization.

THE MOST PROFITABLE ADVANCE IN NEOKINESIS ORIGINATING WITH THE PRIMATES. With the appearance of the primates, the first really profitable advances in neokinesis were actually made. It is probable that the quadrumanal differentiation may have led the early prosimia toward the realm in which the full promise of this motor capacity became possible. In any case, the long awaited instrument, the ready servant of neokinesis, had at length made its appearance. Even with its possession the primates had as yet a long distance to travel, many experimental trials to experience before this new instrument was so adapted as to give its maximum degree of service. The specialization in connection with the upper extremity was a real decisive step forward; but where it extended to the lower extremities and produced feet with many hand-like characters, it immediately imposed serious limitations and created those disadvantages which result from the possession of too many hands. The quadrumanal tendency of the primates positively prohibited the full development of manual differentiation for two reasons: First, it committed the animals to an almost exclusively arboreal life. In the second place, it created a field of psychological indecision which had a profound effect by causing a quandary as to whether the hand should be used as a foot or the foot as a hand. It thus left in indeterminate state an instrument which required above all else the most exact discrimination for its fullest functional differentiation.

PARTING OF THE WAYS BETWEEN ANTHROPOID AND HUMAN. In spite of their early embarrassment due to over-endowment of hand-like characters, the primates had come upon the right trail. It required but one further modification to set them on the track which would lead to the ultimate goal.

This was indeed a critical modification. It established beyond question the great parting of the ways between the anthropoid and the human, raising an effectual barrier between the one kind and the other. It was the decisive influence which turned the course of the apes to their own specific evolutional termini, putting man upon his course which, through various stages of progress, has led to his present estate. What the underlying motive of this critical modification may have been is still clouded in obscurity. The increasing weight of the body appears to have played some rôle in this alteration. For it was unquestionably the development of certain inconveniences and disadvantages in arboreal life that eventually brought some of the primate stock nearer to the ground and finally brought about the change in the lower extremity resulting in the inception of the human foot.

Probable Role of Endocrine Glands. The factors which may have increased the body weight and so necessitated this change from arboreal to terrestrial life are difficult to estimate. It is possible that the endocrine glands had some part in this alteration. Changes in their activity may have so altered the metabolism of the body as to produce that degree of macrosomia which is no longer adapted to tree-dwelling. From pathological evidence it is recognized that enlargements in the pituitary gland produce the condition in man termed gigantism. Many of the more or less monstrous extravagances in statural growth seen often-times in exhibitions and known the world over as giants are the results of hypertrophy in the glandular portion of the pituitary body. That such hypertrophy may well account for an increased secretion in this gland and thus produce exuberant growth in the long bones is an accepted clinical fact. So also is the disease known as acromegaly in which, after adolescence, certain individuals manifest a tendency toward increased growth in the hands and in the feet, in the face and other portions of the bony skeleton, due to alterations in the pituitary gland. Another group of facts pointing in the same direction are those corporeal changes ascribed to diseases of the pineal gland, particularly in the early years of adolescence, producing the condition known as macrogenitosomia praecox or the syndrome of Pellezzi. Under these conditions the individual grows prematurely tall with precocious sexual differentiation. It is the belief that the pineal gland normally holds in abeyance the premature development of the statural and sexual organization by exerting upon the pituitary body an inhibitory influence. Whether these potent factors in control of the metabolic mechanism entered into the causes which produced the critical change in body modification must still be a matter for further investigation. They offer a most enticing suggestiveness. Either they or other similar factors bore some responsibility in these epoch-making changes. In any case, it must have been the near approach to the ground and the final necessity of living upon it which determined the specialization leading to the development of the human foot. At that juncture the embarrassment of over-endowment arising from too much in the way of manual specialization began to dissipate its restrictive influence. With the critical differentiation of the lower extremity in process, with the upright position guaranteed, with the final emancipation of the hand a certainty, the ultimate instrument for extending the boundaries of the neokinetic sphere was at length assured. Too much emphasis cannot be laid upon this decisive change in the two branches of the orthograde division of the primate stem. In consequence of it, the members of one branch retained so much of their arboreal specialization that they continued to be occupants of the forest. Quite the contrary is true of that branch which finally began to stand upright and go upon two feet. Through it, the neopallium now proceeded to externalize all of those potential resources which had so long been held in reserve awaiting the arrival of this ultimate manual equipment. From Pithecanthropus and the Dawn man, from Heidelberg man and the Neanderthal, through all of the achievements of Homo sapiens, the human race has set the full imprint of man's past and contemporaneous record in the vast sphere of neokinesis which has been created as the product of his hands.

RELATION OF MAN TO APES

These are the conclusions drawn from the accumulated evidences concerning an evolutionary process in the brain of the primates. They recognize the development of neokinesis in its several modifications as the keynote of mammalian differentiation. They envision the process of selection and evolution whereby this new type of motor activity, seeking its fullest expression, at length found in the primates those structures from which to develop the achievement of human neokinetic expansion. They take full account of all of the intermediate simian steps in this process, but in no way denote or imply a direct ancestral descent of man from any of the modern apes. In its brain each one of the primates below man has, in its turn, borne the impress of the effort to advance the cause of neokinesis. For this reason, if for no other reason, each infrahuman primate gradation is important in the evolutionary picture. It demonstrates the various attempts at progress showing in what particulars they succeeded and also by just how much they fell short of attaining the final goal. To consider any of the living apes the possible ancestor of man is an inconsequential, trifling and incomplete view of the situation which requires a much more extensive understanding of the biological process for the complete appreciation of its significance. It does not seem sufficient to linger among the modern apes in search of our ancestors. These animals belong to families totally divergent from man. They have become most effectually arborealized, have ascended well up into the trees where doubtless they will remain quite as unconcerned in the origin of man as they are innocent of participation in it.

We are wise if we turn our attention not to these simians, but rather to the generalized mammalian ancestors from which both apes and man took origin, to that stock which may be traced, as Huxley and others maintain, to the organization of some lowly mammal such as the tree-shrew (tupaia). Nor is there reason to pause at this point in the long line of descent. Looking still further back into the past, it is possible to recognize those premammalian reptiles from which the mammals unquestionably descended, as well as their progenitors derived from those low levels of vertebrate organization which gave rise to the great Mesozoic reptilian orders. It is indeed the appreciation of this long ancestral line in all the various modifications of its many geological phases that gives the proper value to the evolutionary process. Perceived in this way, it is possible to sense the full force of the impetus in that irresistible momentum which has carried the great vertebrate phylum upward and onward through the ages and may still carry us onward.

This is a conception that should make an urgent appeal for thoughtful consideration regarding further possible readjustment of human behavior. It is a view of life which requires for its acceptance real powers of vision combined with an open attitude of mind. For now, as in the past, intolerance may resist as rude intrusion any trespass upon its ancient and cherished delusions, prejudice may reject as worthless what it has not itself conceived as true, conservatism may urge a wary hesitation in the acceptance of broad conclusions of any kind. But these facts, correlated here, perhaps for the first time, and standing alone without the aid of commentary or special interpreter, speak in no uncertain terms of a structural unfolding in the brain of primates whose evolutional significance may be seen in the progressive extension of their behavioral capacities. In this aspect these factors may appear merely as a conventional formulation of scientific deductions. They may fail entirely to create an impression of the actual dynamic force which lies behind them. It is for this reason and by virtue of having essayed to answer so many queries, that the writer feels privileged to ask a question of his own. It touches a vitally important problem, and may be phrased as follows:

Is there still a possibility of further evolving in the developmental process so clearly seen in the brain of primates, so obviously reaching its present culmination in the brain of man is there still a latent power in the human brain for the expression of yet unsuspected potentialities and beneficial progress?

This is a question which may not be quickly read or soon forgotten. There is an undeniable insistency about it as it calls attention to the palpable imperfections in human organizations. Answered in the negative, to what continuing discouragement does it not commit the race; answered in the affirmative, with what inspiring expectations may we not look to the future of mankind! This greatest problem of humanity is susceptible of solution. It awaits only the intelligence, the patience, the persistency and the determination to solve it.

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WYATT, H. G. Intelligence [illegible] *Ps*[illegible] *R*[illegible] P[illegible] 192[illegible]
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