I—The Brain-Stem and Cerebellum of *Echidna aculeata*

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(Communicated by G. Elliot Smith, F.R.S.—Received March 16—Read June 21, 1934)

Descriptions of the brain of *Echidna* are almost lacking in modern literature. Of the older accounts, those by Ziehen (1897, *a* and *b*; 1901, 1908), Kölliker (1901), and Elliot Smith (1899, 1902) are the most important. More recently, descriptions of isolated structures have appeared in accounts of the phylogeny of these. Thus Van Valkenburg (1911) has described the mesencephalic nucleus and root of the fifth nerve, Kooy (1916) the inferior olive, and Schepman (1918) the eighth nerve. In addition, Fuse (1926, *a*, *b*, *c*, *d*, and *f*) has published a series of papers on various structures in the medulla oblongata including the nucleus arcuatus, the nucleus of the "Zonalbündel," the "Zonalbündel" itself, the lateral nucleus of the lateral fasciculus of the medulla oblongata, the superior olive, and the tuberculum acusticum.

Although no recent paper deals with the fore-brain it is known that the great size of the cerebral hemispheres owes very little to the olfactory system and even less to the visual apparatus. Since any explanation based on the hypertrophy of the trigeminal nerves does not account for the increased size of the cerebrum as contrasted with that of *Ornithorhynchus*, it is felt that a study of lower centres must precede a detailed investigation of the fore-brain. This study reveals that some of the features of the hemispheres are explicable from the development of the lower centres.

An extensive account of the brain of *Ornithorhynchus* has recently been published by Hines (1929). This has been used as a basis of comparison, and some of the differences in interpretation are the result of the possibility of such comparison. The only other mammals at all closely connected with *Echidna* are the marsupials. In the works of the American neurologists we have a very complete record of the structure of the brain of *Didelphys virginiana* and, wherever possible, comparisons have been instituted with their descriptions.

No attempt has been made to review the whole of the literature on the various sections described here. Only the most representative papers are quoted and most of these survey the relevant literature very thoroughly. Throughout this work

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VOL. CCXXIV.—B 509 (Price 9*s*. 6*d*.) B [Published October 30, 1934.

reference was made to the atlases of WINKLER and POTTER on the brain of the rabbit (1911) and cat (1914) ; in addition, the treatise by KAPPERS (1920) was freely consulted.

MATERIAL

This investigation was undertaken at the suggestion of Professor KAPPERS, and I should like here to express my gratitude for the kindness he has shown in placing at my disposal the resources of his Institute, in many valuable suggestions as regards literature and in his continuous interest in the progress of the work. At the same time I must also acknowledge with thanks the many services received from Dr. J. L. ADDENS, of this department.

Of the material available, the following were finally selected for study :—

1—A transverse series, formerly the property of Professor Th. ZIEHEN, stained after Weigert-Pal. This extended to the mid-habenular region but was incomplete and many of the sections were badly damaged. Two slides from this series were drawn for reproduction.

2—A transverse series similarly stained which belonged originally to Professor SYMINGTON. These were very good but, unfortunately, many were missing.

3—A complete transverse series stained after Weigert-Pal and with paracarmine. These extended from the lower part of the first cervical segment of the cord and form the material from which most of the drawings were made. The presence of a large amount of moisture in the mounting medium, however, rendered many of the slides of this series unsuitable for high-power examination.

4—A complete sagittal series beautifully stained after Weigert-Pal and counter-stained alternately with paracarmine and alum-carmine. These were of the greatest assistance in checking the transverse sections.

5—Some sections stained by Nissl's method and others with hæmatoxylin were also available. The Nissl's sections were too faded to be of any assistance. Most of the hæmatoxylin sections were not in good condition, but it was possible in some cases to use them to confirm or disprove the impressions gained from the Weigert series.

6—Professor KAPPERS generously allowed me to dissect two of the *Echidna* brains which were presented to him by Professor BURKITT, of Sydney. The gross drawings were made from both of these. A close examination of the other three specimens—two of which were already partly dissected—was of great assistance in the study of the cerebellum and geniculate bodies.*

All the slides reproduced were drawn with the aid of the Edinger projection apparatus. Finer detail was added from direct observation under higher magnification.

THE MEDULLA OBLONGATA

The ventral surface of the medulla oblongata is very broad, fig. 3. This breadth is due to the great size of the tuberculi quinti which project at the ventro-

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* Since my return I have had the opportunity of examining four more *Echidna* brains at University College, London. One of these I dissected and confirmed the present description.

lateral angles. The tuberculi narrow considerably and pass dorsally as they approach the cord. Medial to each tuberculum is a groove which separates it from the eminentia olivaris, and medial to this the inconspicuous swelling of the pyramidal tract. Many large bands of external arcuate fibres cross the ventral surface of the medulla oblongata. These appear to be discrete, but microscopic examination reveals them as a continuous series from the pons to the caudal border of the medulla oblongata. The poorly developed pyramids are considerably obscured in the mid-line by the crossing external arcuate fibres and present the appearance of a diffuse decussation. This is not, however, the decussation of the pyramids for that lies at the junction of medulla oblongata and cord and is quite compact, fig. 7.

The root fibres of the abducent and hypoglossal nerves define the lateral borders of the pyramids. The sixth nerve emerges at the caudal border of the pons as a single root, the hypoglossal nerve lies more posteriorly and comprises eight to ten large roots. The spinal part of the accessory nerve passes forwards from the cord to join its cranial component, and just anterior to this are the vagus and glosso-pharyngeal nerves which are attached to the dorso-lateral part of the tuberculum quinti immediately ventral to the flocculus. The eighth nerve is attached at the posterior border of the pons. It is large and readily separable into cochlear and vestibular divisions. The cochlear constitutes about one-third of the total bulk of the eighth nerve and its fibres are smoother and more compact than those of the vestibular division. The cochlear nerve lies dorso-lateral and posterior to the vestibular nerve. The seventh nerve emerges at the posterior border of the pons and just medial to the entrance of the eighth nerve, figs. 1 and 3.

The eminence of the gracile and cuneate nuclei forms a large swelling at the anterior end of the posterior funiculus of the cord. These swellings extend anteriorly

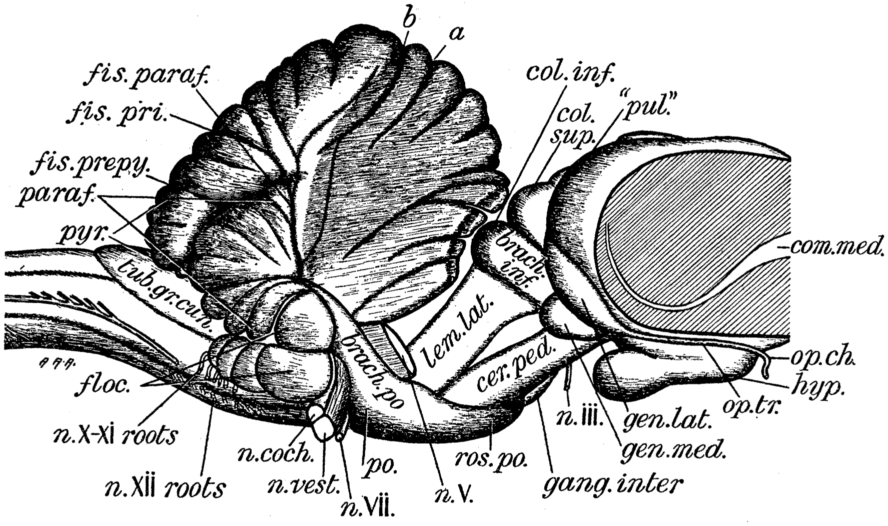

FIG. 1—Lateral aspect of the brain-stem and cerebellum. × 4. Note the large lobus anterius and paraflocculus in the cerebellum ; the large fifth and eighth nerves ; the medial and lateral geniculate bodies and the caudal projection of the " pulvinar."

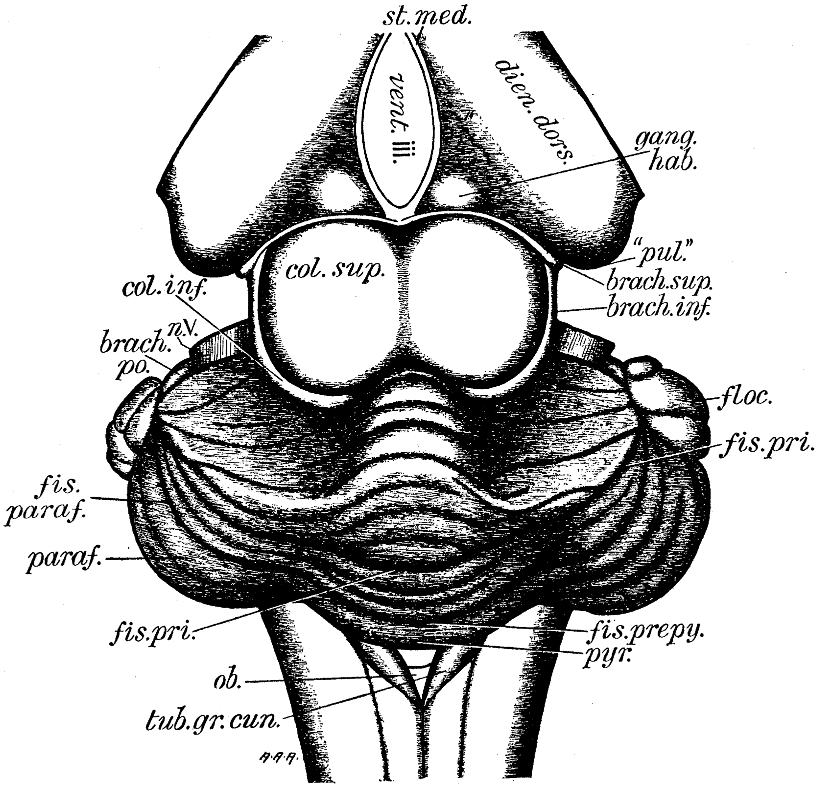

Fig. 2—Dorsal aspect of the brain-stem and cerebellum. × 4. The caudal projection of the posterior poles of the thalami is obvious. The ganglia habenulæ form conspicuous prominences. The large superior colliculi are in sharp contrast to the thread-like superior brachia. The caudal prominence of the lateral lobes of the cerebellum is due almost entirely to the size of the paraflocculi.

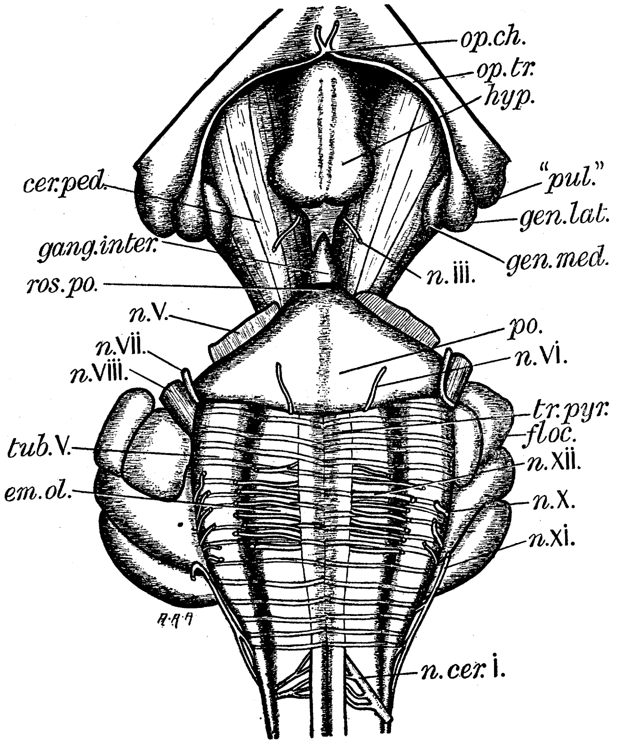

Fig. 3—The ventral aspect of the brain-stem. × 4. The optic tracts and chiasma are tiny. Note that the crus pontis lies entirely caudal to the fifth nerve. The external arcuate fibres form a continuous layer over the ventral surface of the brain-stem.

on each side of the fourth ventricle but present no external indication of any separation into component nuclei. Between the eminences lies a well-defined obex, fig. 2.

The Motor Systems of the Medulla Oblongata

The Hypoglossal Nerve—The nucleus of this nerve is large as would be expected in an animal whose tongue plays such an important part in its daily economy, fig. 8. Posteriorly it can be traced in tenuous continuity with the anterior horn cells of the spinal cord, anteriorly it extends almost to the level of the anterior pole of the dorsal vagal cell column. This nucleus is, therefore, typically mammalian in disposition. Posteriorly it has not attained its most dorsal position at the level of opening of the fourth ventricle, fig. 7; this led Kölliker (1901) and Ziehen (1908) to assume that the fourth ventricle opens more caudally in *Echidna* than in other mammals. The ventral situation of the posterior part of the hypoglossal nucleus appears to be a primitive feature for the opening of the fourth ventricle occurs at about the same level as in any other mammal. After the main mass of the hypoglossal nucleus has reached its dorsal situation there is an anterior extension of some of the ventrally-lying cells which contribute fibres to the emerging hypoglossal roots. This remnant indicates the line of dorsal migration.

The main hypoglossal nucleus is large and broad, and flattened dorso-ventrally as in the opossum (Kappers (1920), Voris and Hoerr (1932)). It does not, however, occupy the usual mammalian position dorsal to the medial longitudinal fasciculus but lies lateral to this. The cells are very large and of the motor type. The root fibres emerge from the ventro-medial border of the nucleus and, passing ventrally with a slight medial convexity, separate the inferior olive and lateral reticular nucleus to emerge in close relation to the large arcuate nucleus, fig. 8. The pyramidal fibres enter the nucleus from its medial aspect.

From the lateral aspect of this same cell column arise fibres which run laterally and slightly ventrally to join the vagus nerve. More anteriorly this lateral part becomes separated from the main cell column, fig. 8. This is not a separate nucleus for its cells are of exactly the same type as those of the hypoglossal nucleus and posteriorly are continuous with these; nor does it represent the small-celled accessory hypoglossal nucleus of Roller.

The presence of vagal fibres arising from a cell column which is composed chiefly of hypoglossal cells is of particular interest in view of the findings of Addens (1933). This author has shown that in the development of the bird the nucleus ambiguus has a double origin. It is formed partly by a ventral migration of cells from the dorsal vagal cell column in the usual manner, but also receives a contribution of ventrally migrating cells from the column which gives rise to the hypoglossal nucleus. Under these circumstances the lateral part of this cell column in *Echidna* must be considered an undescended component of the nucleus ambiguus, and in this respect *Echidna* resembles a developmental stage of birds. Such an occurrence has not, I believe, been recorded previously. The undescended portion of the nucleus ambiguus receives pyramidal fibres in the same manner as does the hypoglossal nucleus.

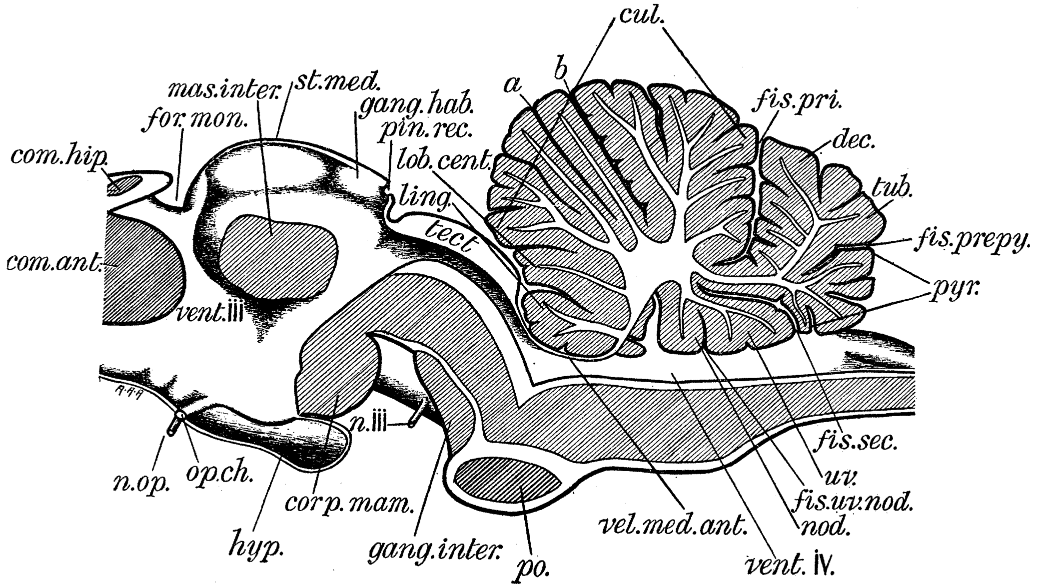

FIG. 4—Median section through the brain-stem and cerebellum. × 4. This illustrates the enormous size of the lobus anterius of the cerebellum. The large hypophysis, corpus mamillare, and ganglion interpedunculare are well shown. Note the relation of the optic chiasma to the infundibulum.

The Accessory, Vagus, and Glossopharyngeal Nerves—The dorsal vagal cell column extends from the caudal border of the medulla oblongata to the level of the vestibular nerve. Posteriorly the columns of both sides approach the mid-line and are continuous in the commissural nucleus of CAJAL, fig. 7; anteriorly they are pushed laterally and ventrally by the expansion of the principal vestibular nucleus and come to lie just medial and ventral to the nucleus of DEITERS, fig. 9. This anterior portion was called the *nucleus glossopharyngei* by KÖLLIKER (1901) for *Echidna* and *Ornithorhynchus* and by HINES (1929) for *Ornithorhynchus*. It appears to be merely the anterior pole of the dorsal vagal cell column. This column comprises a dorsal small-celled part and a ventral large-celled portion. It is separated from the hypoglossal nucleus and the undescended portion of the nucleus ambiguus medially by the *nucleus intercalatus* of STADERINI which enlarges anteriorly to become the principal vestibular nucleus.

The nucleus ambiguus is composed of motor cells smaller than those of the hypoglossal nucleus and extends almost as far anteriorly as the dorsal nucleus. As in the opossum the posterior part of this nucleus is poorly developed and is represented by a very few cells in any section. Anteriorly it enlarges considerably and presents a compact cell mass, fig. 8. The small size of the nucleus is due in part, no doubt, to the retention of some of its elements with the hypoglossal nucleus.

The fasciculus solitarius appears first at the level of the seventh nerve some of whose fibres appear to form its anterior end. More caudally it lies lateral to the anterior pole of the dorsal vagal nucleus where the ninth nerve arises. Many fibres from the glossopharyngeal nerve pass to the fasciculus and increase its bulk considerably. In its posterior passage the fasciculus migrates dorsally and medially with the dorsal vagal nucleus and continues to enlarge until it forms a very conspicuous bundle, fig. 8. It is accompanied by dorso-lateral and ventro-medial nuclei. Fibres pass from the anterior extremity of the fasciculus to the opposite medial lemniscus, from its posterior extremity to the *commissura infima*.

The nucleus intercalatus of STADERINI is interposed between the dorsal nucleus of the vagus and the hypoglossal nucleus, fig. 9. It is composed of very small cells and widens anteriorly into the principal vestibular nucleus. In *Echidna* there is no indication of any separation of the two nuclei, the nucleus intercalatus is simply a caudal extension of the principal vestibular nucleus. This is in agreement with the findings of STOKES (1911) and VORIS and HOERR (1932) for the opossum, and contrary to those of STREETER (1903) for Man.

The efferent root-fibres of the accessory, vagus, and glossopharyngeal nerves arise from their nuclei and pass laterally and slightly ventrally through the descending root and nucleus of the fifth nerve to emerge from the dorso-lateral aspect of the tuberculum quinti just below the flocculus, fig. 8. There is no intracerebral distinction between vagus and the cranial portion of the accessory.

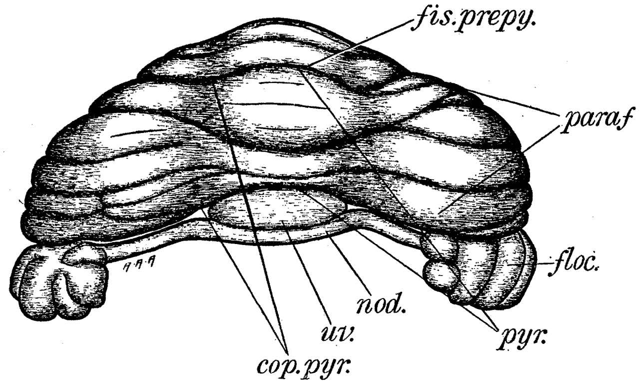

FIG. 5—Postero-inferior view of the cerebellum. × 4. The large pyramid is clearly continued laterally into the paraflocculi. The nodule is continuous with the flocculi. The uvula has no relation to any part of the cerebellar hemispheres.

The Seventh Nerve—The facialis nucleus of *Echidna* is usually described as comprising separate dorsal and ventral parts as in the Sauropsida. There is, in fact, only one facialis nucleus. This is very large and extends caudally almost to the anterior pole of the nucleus ambiguus ; frontally it reaches the level of maximum development of the fifth motor nucleus, fig. 13. The seventh nucleus has not yet attained that characteristically ventral position which appears first in marsupials, and it still lies dorsal to the superior olive, fig. 11. In the opossum it lies on a level with, and posterior to, the superior olive. The cells of the nucleus are very large.

The posterior part of the seventh nucleus is massive, fig. 10. As it extends forwards it ascends slightly and at the level of the anterior pole of the sixth nucleus divides to be continued in dorsal and ventral projections. These pass anteriorly, the dorsal part ascending more abruptly than the ventral so that they continue to diverge. Both divisions can be followed, fig. 11, to the medial side of the fifth motor nucleus where they gradually disappear. The dorsal division is much the larger, although this is not seen in the sections figured, and extends slightly more anteriorly than the ventral. For some distance scattered cells can be found connecting the two divisions, but these eventually fail and the parts appear to be independent. It is to this appearance that the current description of separate dorsal and ventral nuclei is due. The facialis nucleus is, then, V-shaped. The caudal main mass represents the apex of the V, the diverging frontal extensions the limbs of the V which is open anteriorly. This peculiar distribution of the seventh nucleus appears to be the result of an arrest of ventral migration at an intermediate stage.

The ascending limb of the seventh nerve runs dorsally and slightly medially to its genu which lies for the most part ventral to the sixth nucleus, although some of the cells of this are scattered amongst the fibres. The ascending fibres from the dorsal extension pass more directly to the descending limb, fig. 12. The genu passes forwards for a short distance and then turns laterally to form the descending limb. This runs laterally and slightly ventrally to pass through the dorsal part of the descending root and nucleus of the fifth nerve in series with the glosso-pharyngeal, vagus, and accessory nerves. The seventh nerve emerges from the dorso-lateral part of the tuberculum quinti medial to the eighth nerve at the posterior border of the pons. Some fibres from the seventh nerve join the anterior end of the fasciculus solitarius, they probably carry gustatory and, possibly, general sensory impulses.

The large size of the seventh nucleus in the Monotremes, and especially in *Echidna*, has been correlated by the late ERNST HUBER (1931) with the extraordinary development of the facialis musculature in these animals. In the Monotremes the second arch musculature invades the face region for the first time, and also extends far posteriorly to join the panniculus carnosus muscle and to be inserted into the bones of the fore-limbs. In the Sauropsida the facial region is practically free of hyoid arch musculature which is represented in them chiefly by the primitive sphincter colli and depressor mandibulæ muscles.

The Sixth Nerve and Accessory Sixth Nucleus—The sixth nucleus is represented by scattered small motor cells which lie ventral to the principal vestibular nucleus and extend to the lateral angle of the fourth ventricle, fig. 9. Medially the cells lie amongst, but chiefly dorsal to, the genu of the seventh nerve. Posteriorly the mass falls short of the caudal border of the seventh nucleus ; anteriorly it reaches the level of division of this into dorsal and ventral extensions.

The sixth nerve is small—probably in correlation with the generally poor visual development (this generalization does not hold, however, for the oculomotor nucleus)—and its fibres pass directly ventrally, medial to the seventh nucleus and the superior olive, and emerge at the lateral border of the pyramid, fig. 11. The peduncle of the superior olive runs dorsally, lateral to the emerging sixth root, to join the abducens nucleus.

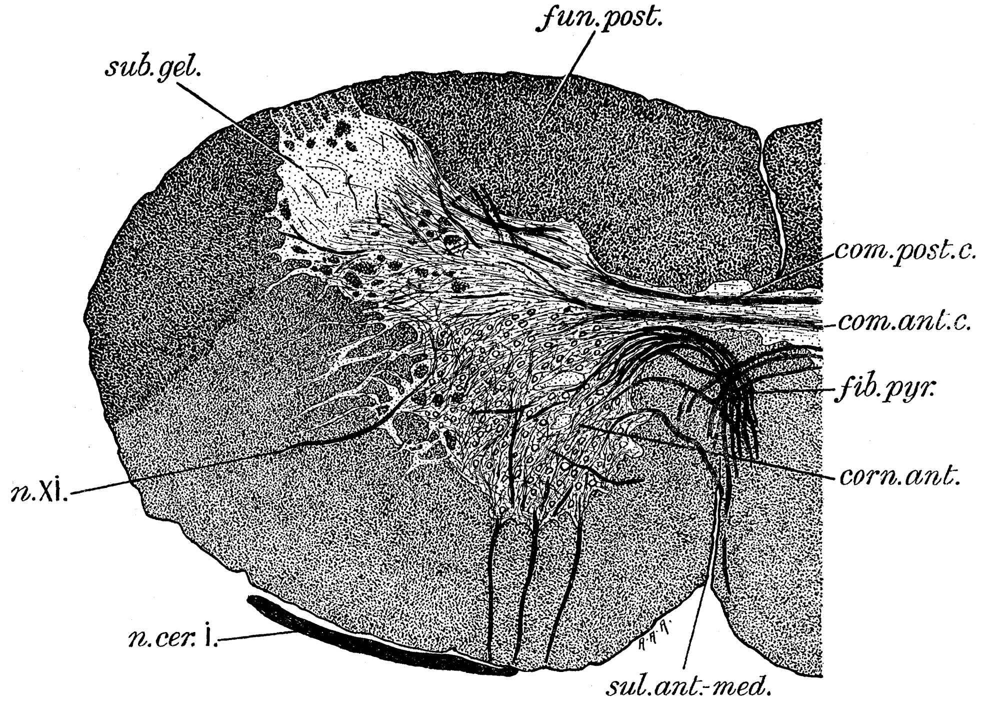

FIG. 6—Transverse section through the upper part of the cervical cord. × 20. The pyramidal fibres cross dorsal to the raphe to reach the opposite anterior horn where they end directly around the motor cells. The decussation is well separated from the anterior commissure. No pyramidal fibres reach either the lateral or the posterior funiculus. Note the size of the posterior funiculi.

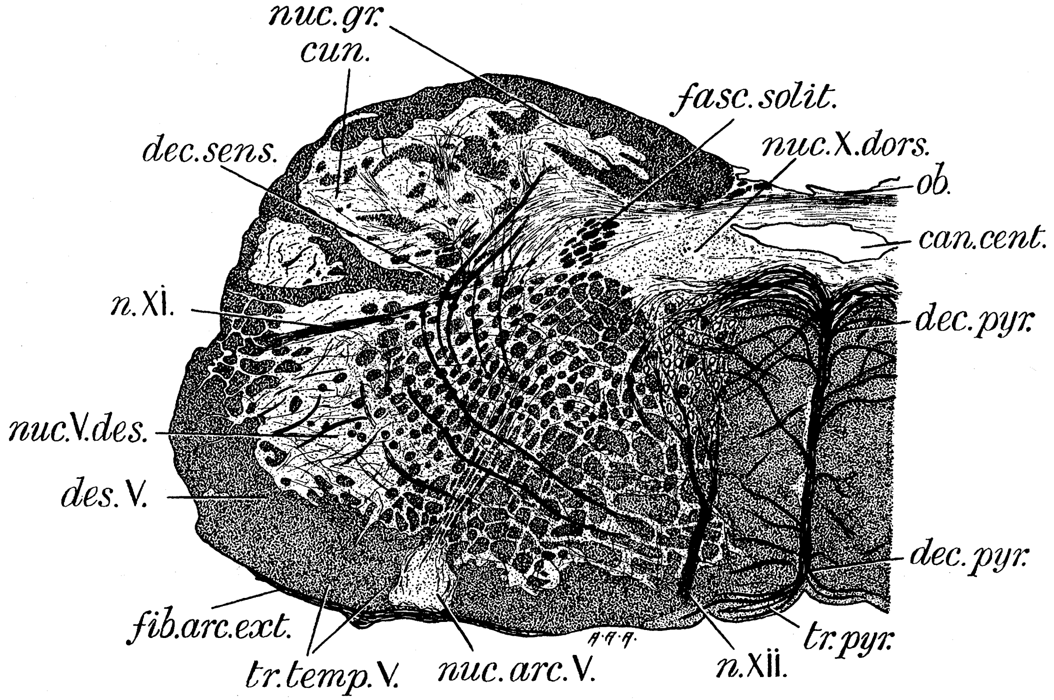

FIG. 7—Transverse section through the closed part of the medulla oblongata. × 10. This is through the pyramidal decussation and shows the fibres ascending the raphe to reach the opposite hypoglossal nucleus, which has not yet reached its most dorsal situation. The combined gracile and cuneate nuclei form a mass equal in size to the nucleus of the descending root of the fifth nerve.

About midway between the sixth and seventh nuclei, and at a level which more anteriorly corresponds with that of the dorsal division of the seventh, lies a small compact collection of cells of type similar to those of the sixth nucleus, fig. 10. This nucleus does not extend as far anteriorly or posteriorly as the true sixth nucleus and is separated from the dorsal extension of the seventh nucleus by a distinct interval. This mass is almost certainly the accessory sixth nucleus. It belongs to neither the sixth nor the seventh nucleus and its relation to both is characteristic of the accessory sixth nucleus of other animals.

TERNI (1921) has described an accessory sixth nucleus in fishes, reptiles, birds, and mammals. He describes for Sauropsida a " riflesso trigemino-abducente " or " riflesso di chiusura " (1922) which is initiated by stimulation in the peripheral distribution of the fifth nerve and mediated by connections between the descending root of the fifth nerve and the accessory sixth nucleus. This reflex is manifested by retraction of the bulbus oculi and closure of the lids. PREZIUSO (1924, 1930) has found an accessory abducens nucleus in some birds and mammals, and ADDENS (1933) has made it clear that such a nucleus is probably present throughout the vertebrate series including amphibia, in whom the reflex is most readily elicited. An accessory sixth nucleus was not, however, described by HINES (1929) for *Ornithorhynchus* nor by VORIS and HOERR (1932) for the opossum.

The Pyramidal Tracts—The pyramidal tracts were described in their superficial course by ELLIOT SMITH (1902) and by ZIEHEN (1897, *a*). KÖLLIKER (1901) and ZIEHEN (1897, *b*, 1908) both recognized a pyramidal decussation at the posterior part of the medulla oblongata. The pyramids can be seen on the ventral surface of the medulla oblongata, fig. 3, in the position characteristic for all mammals. They are small, it is true, but large pyramids would not be expected in so primitive a mammal. The pyramids in the opossum as described by TURNER (1924) and VORIS and HOERR (1932) are by no means large.

It is necessary to emphasize from the outset that the pyramids in *Echidna* pursue the usual mammalian course, for FUSE (1926, *f*) has recently denied that the decussation described by KÖLLIKER and ZIEHEN is of a pyramidal nature. He dismisses their description in a footnote (p. 97) thus : " Nach Kölliker ist bei Echidna ein besonderes Pyramidenbündel an der ventralen Selte (? Seite) des Fasciculus ventralis schon von Anfang an sicher nicht umgrenzt vorhanden und später gar nicht nachzuweisen. Trotzdem erkennt er dabei eine schwach ausgebildete Pyramidenkreuzung, ohne jedoch ihre Herkunft feststellen zu können. Nach Ziehen der bei Echidna eine Zone feiner, ziemlich zerstreuter blasser Fasern unmittelbar neben der Raphe als Pyramidenbahn annimmt, lässt sich ihre distale Kreuzung nicht deutlich bestimmen. Nach meiner Beobachtung ist die Köllikersche Pyramidenkreuzung kineswegs der bulbären d.h. distalen der Säuger gleichzustellen ; sie stellt vielmehr ein Fasersystem der Commissura anterior dar, welches auch bei den übrigen Säugern vorkommt." Thus FUSE considers that the decussation described by KÖLLIKER is merely part of the anterior commissure of the spinal cord. In his opinion the pyramids in *Echidna* are represented in the

" Zonalbündel " of **Kölliker** (tractus temporo-trigeminalis of this paper) and he classifies them as variety 2 in his list of possible pyramidal decussations (**Fuse** (1926, *g*)). It will be best to describe the pyramidal tracts before examining this statement more closely.

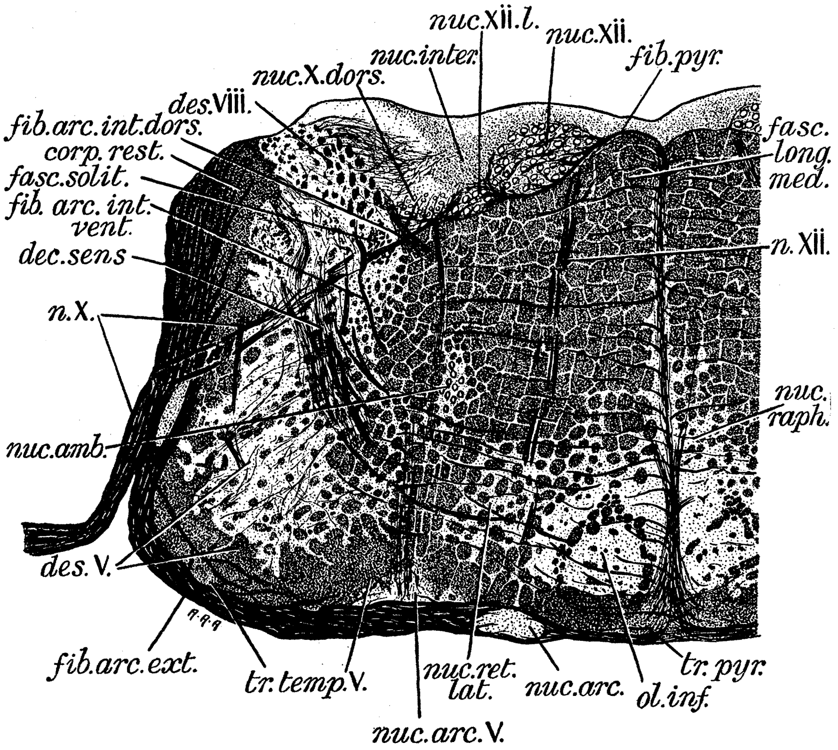

Fig. 8—Section through the open part of the medulla oblongata. × 10. Note that part of the nucleus ambiguus retains a dorsal situation at the lateral side of the hypoglossal nucleus. Dorsal and ventral internal arcuate fibres can be seen. The nucleus arcuatus trigemini is closely related to the external arcuate fibres, the dorsal and ventral internal arcuate fibres, the descending root of the fifth nerve and the tractus temporo-trigeminalis.

In the cerebral peduncles above the pons the true pyramidal tracts can be distinguished as a small bundle of fine, lightly-stained fibres lying at the medial border of the peduncle and closely related to the substantia nigra, fig. 16. When the peduncles reach the pons the medially lying pyramids are the first to enter the rostrum, fig. 15. They pass at once to the ventral border of the medial lemnisci, fig. 13, and maintain this relation throughout their subsequent passage in the brain-stem. Below the pons the pyramids are distinguishable by the fineness of their fibres, figs. 9 and 10. The external arcuate fibres pass through and around the pyramids and greatly obscure this small bundle. In the Weigert-Pal carmine series, however, the pyramids lay quite free on the surface superficial to the trapezial fibres, fig. 9 ; this figure—as far as the relation of the pyramids to the corpus trapezoideum is concerned—might have been drawn from the brain-stem of any primitive mammal. But in the greater part of their course the pyramids are obscured by the crossing external arcuate fibres for they are not yet sufficiently well developed to dominate the picture.

The decussation of the pyramids was described very vaguely by ZIEHEN and KÖLLIKER. In 1897 ZIEHEN said : " There is no pyramidal crossing in the usual sense, in place of this there is a raphe in which both fibre bundles ascend in regular order." He says that these bundles come from the *lateral funiculi*, pass through the anterior horn and anterior funiculi and bend ventrally in the region of the raphe. Then they cross in very acute angles and collect at the medial side of the anterior funiculus. Except that the pyramids have no relation to the lateral funiculi whatever, this is the exact opposite of what actually occurs. In his later paper in 1908 ZIEHEN was not sure whether the pyramids lie in the most dorsal part of the lateral funiculus. In 1901 KÖLLIKER merely pointed out that a pyramidal decussation occurs and said (p. 83) that the decussation is composed on each side of three or four bundles whose origin, whether from the *lateral funiculus* or *funiculus cuneatus*, is doubtful. Before examining the actual decussation of the pyramids it will be well to describe the method by which pyramidal fibres reach some of the cranial motor nuclei since this has a distinct bearing upon the ultimate mode of decussation.

Pyramidal fibres could be traced with certainty to the seventh and hypoglossal nuclei, less surely to the sixth nucleus and the nucleus ambiguus. In the region of the seventh nucleus, fig. 9, pyramidal fibres pass to the raphe in which they ascend for about one-third of its extent before passing out to the opposite facial nucleus. The decussation of these fibres may occur at the base of the raphe, or just before the fibres leave it, or anywhere in between, but appears to be complete. This differs in degree only from KAPPERS' (1920) description of the decussation of the facialis pyramid in the bat. In this animal the seventh nucleus lies more ventrally than in *Echidna* and the decussation occurs at the base of the raphe, the fibres then pass directly laterally to their destination. (Through the kindness of Professor KAPPERS I have had an opportunity of examining the slides of the bat in question. It is clear from these that the sole difference from the condition in *Echidna* is correlated with the more ventral situation of the seventh nucleus in the bat and the consequent more direct crossing of the pyramidal fibres.) Some pyramidal fibres appear to reach the apex of the raphe in this region there to cross before passing laterally. They appeared to reach the sixth nucleus, but it was impossible to be certain of this.

In the region of the hypoglossal nucleus the raphe is very thick and contains many ascending pyramidal fibres, fig. 8. These can be traced from the pyramidal tracts to the apex of the raphe where most cross and pass to the opposite hypoglossal nucleus including that lateral extension which represents an undescended portion of the nucleus ambiguus. Some fibres pass more directly to their destination. A few of these dorsally decussating fibres appear to pass beyond the hypoglossal nucleus to reach the ventral part of the nucleus ambiguus.

At the caudal limit of the medulla oblongata the chief pyramidal decussation occurs, fig. 7. Bundles of fibres ascend on each side of the raphe and cross at the apex to reach the anterior horn cells of the opposite side. (In fig. 7 the anterior horn cells really represent the caudal end of the hypoglossal nucleus.) Some fibres cross more ventrally and pass directly to the anterior horn. Not all the fibres cross immediately ; many collect on each side of the raphe where they run caudally, fig. 6, crossing to reach the opposite anterior horn as they go until they are finally completely dissipated. The pyramids certainly reach to the lower part of the first cervical segment, but it is doubtful whether they pass very much lower. The decussation appears to be complete and the fibres end directly around the anterior horn cells.

It can be seen that FUSE is completely in error when he denies the pyramidal nature of this crossing ; nor could it be confused in any way with the anterior commissure of the cord as he supposes for this lies dorsal to, and quite separate from, the decussation, fig. 6. At no stage of their course do the pyramidal fibres run in the posterior or lateral funiculi as described by ZIEHEN and KÖLLIKER. They are related entirely to the anterior funiculi which they leave only to reach the opposite anterior horn.

HINES gives no description of the pyramids in *Ornithorhynchus*, but the description and figures by KÖLLIKER and ZIEHEN and the sections which I have examined make

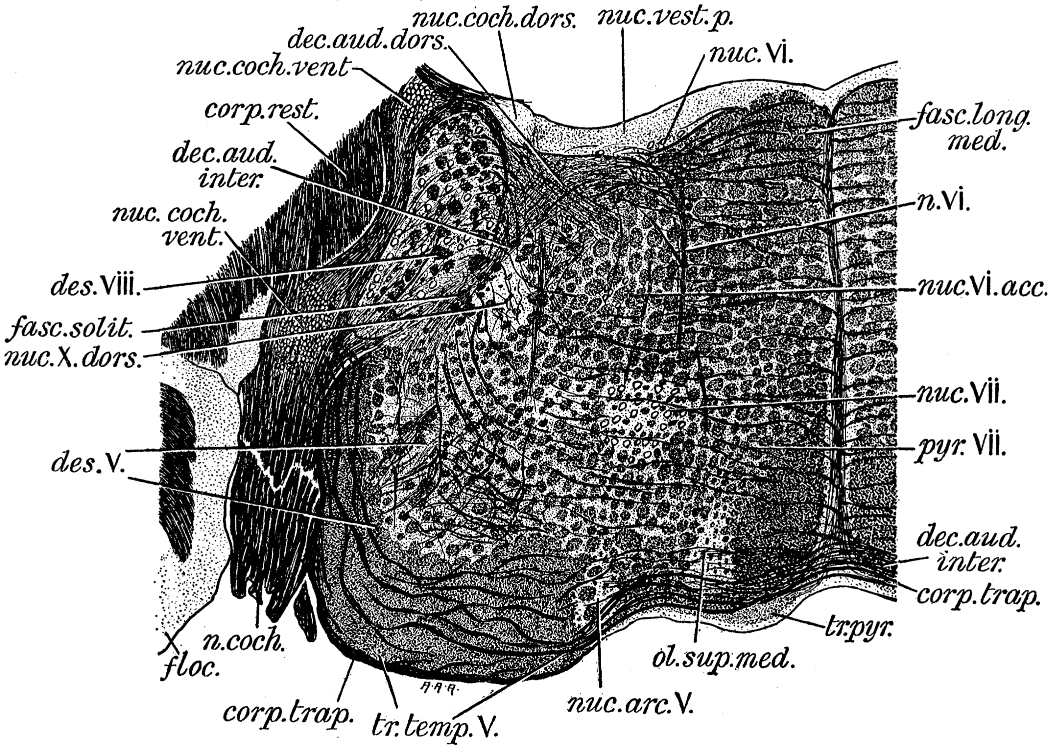

FIG. 9—Section through the level of entrance of the cochlear nerve. × 10. The dorsal situation of the corpus restiforme, the three auditory decussations, the superior olive and the large facialis nucleus are all illustrated. The corpus trapezoideum is very small and most of the fibres which pass in it reach the corpus restiforme.

it clear that they are very similar to those in *Echidna*. In the Monotremes the pyramidal tracts have a very restricted course and a primitive mode of termination. They run in the anterior funiculus for a short distance only and leave it just before they terminate ; and they end by passing to the opposite anterior horn where they come into direct relation with the motor cells. This type of pyramid resembles closely that described by FUSE (1926, *g* and *h*) for the hedgehog, mole, and horse. TURNER (1924) has shown that in the opossum, although the majority of pyramidal fibres pass to the posterior funiculi after decussation, a definite proportion run uncrossed in the anterior funiculi and decussate only when they pass to the opposite anterior horn where they end directly around the motor cells. The so-called direct pyramidal tracts in Man and the higher Primates pursue a similar course. FUSE has shown that this direct tract is by no means restricted to the higher Primates, and FLECHSIG regarded it as phylogenetically older than the indirect.

The only pyramidal tracts that the Monotremes possess are similar in course and termination to the direct pyramids of other mammals. In Man and the higher Primates these direct tracts extend to the mid-thoracic region, but it is doubtful if they reach below the upper cervical segments of the cord in the Monotremes. The fact that MARTIN (1898) obtained movements of the forelimbs by cortical stimulation in *Ornithorhynchus* does not disprove the pyramidal nature of this tract, for HUBER showed that the facialis musculature in both Monotremes is inserted into the bones of the forelimbs.

In most higher mammals the majority of the pyramidal fibres cross at the caudal border of the medulla oblongata and pass either to the posterior funiculi (as in most marsupials, some rodents, insectivores, and ungulates) or to the lateral funiculi (as in some marsupials and most of the higher mammals including Man). KAPPERS has shown in many papers, and the evidence is admirably summarized in his classical treatise (1920), that the passage of pyramidal fibres to the posterior and lateral funiculi is probably due to the neurobiotactic influence of the sensory centres which lie there. The crossed pyramidal tracts appear to act upon the anterior horn cells through the intermediation of these sensory centres. But in many mammals there is, in addition, this direct pyramidal tract which has no relation to the sensory centres but passes directly to the anterior horn cells.

We must conclude, then, that the primitive Monotreme type of pyramid probably occurs in most mammals but is never the dominant motor system. It appears to be an experimental type which, although extended in higher mammals, was not so successful as the indirect pyramid. This appears to have gained in efficiency from its association with sensory centres and the consequent immediate correlation of sensory with motor impulses. Thus the indirect pyramid has come to supersede to a great extent the more primitive and less efficient direct pyramid.

THE SENSORY AND CO-ORDINATION SYSTEMS

The Gracile and Cuneate Nuclei—ZIEHEN describes these as small. They are, on the contrary, extraordinarily large. The combined gracile and cuneate nuclei form a large, well-laminated mass, fig. 7, which produces a marked swelling on the surface, fig. 1. It is impossible to make any distinction between the two nuclei ; the most medial part extends more caudally and probably represents the gracile nucleus. Anteriorly the whole mass expands enormously so that in transverse section it occupies an area as large as, or larger than, that of the nucleus of the descending root of the fifth nerve. (See fig. 7, where the gracile-cuneate mass has not yet attained its maximum proportions.) An estimate* of the proportion of the white matter in the posterior funiculi to total white matter in the cord gave an average result of 25 per cent. This figure would be extremely high for any mammal, especially when one takes into account the large size of the descending fifth root which goes to swell the lateral funiculus.

Brouwer (1915) has estimated the proportion of white matter in the posterior funiculi in a large number of animals. His figures show that the percentage rises in an ascending phylogenetic scale. Outside the higher Primates only the elephant and porpoise exceed the proportion of 25 per cent, and in both the large surface area of the body would provide an explanation for the high figure. In the higher Primates the proportion tends to exceed 25 per cent, and in Man is nearly 39 per cent. For *Tarsius* and *Hapale* Woollard (1928) gives figures of 20 and 25 per cent respectively, and he concludes that the proportion is an index of the degree of epicritic development. *Echidna* lies very low in the phylogenetic scale and its small surface area affords no explanation for this exquisite sensory development which ranks it with the highest Primates. It is necessary to postulate some physiological extension of the surface area, and it is probable that the spiny coat serves such a purpose. As far as I am aware, there has been no investigation of the possible existence of specialized nerve-endings associated with these spines.†

The sensory decussation first appears at the anterior level of the pyramidal crossing. It soon becomes very large and gradually fades away anteriorly. The fibres pass chiefly to the opposite medial lemniscus which forms in and around the inferior olive, fig. 8. Other fibres end in the inferior olives of both sides, while some become external arcuate fibres. Dorsal external arcuate fibres are also given to the corpus restiforme of the same side, fig. 8. Thus, in addition to forming a very large infra-trigeminal lemniscus, the gracile and cuneate nuclei contribute abundantly to the cerebellum.

In *Ornithorhynchus*, according to Hines, the gracile and cuneate nuclei and the medial lemniscus are similarly greatly developed. It must be assumed that tactile sensibility plays a large part in the daily life of both animals. In this respect a quotation by Elliot Smith (1895, p. 342) concerning *Ornithorhynchus* may be applied

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* This was made by projecting an upper cervical section of the spinal cord on millimetre-squared paper with the Edinger apparatus. The outlines of the white matter were traced and the proportion in the posterior funiculi calculated by counting the number of square millimetres in each area.

† Professor J. T. Wilson, of Cambridge, has suggested that this great sensory development may be due to muscle sensibility in view of the exquisite control over the panniculus carnosus muscle which *Echidna* exhibits.

in part to *Echidna :* " It can easily be conceived that as the animal spends much of its time in dark, subterranean channels, where impressions of sight and hearing avail little, that the sense of touch should be of most service, and, together with the sense of smell, should be a guide sufficient to the needs of this strange creature."

The Trigeminal Apparatus—The trigeminal system in *Echidna*, while not as large as that in *Ornithorhynchus*, betrays, nevertheless, the same type of specialization. E. Huber (1930) has shown that in both Monotremes the foramina in the skull for the peripheral distribution of this nerve differ entirely in arrangement from those in all other mammals. In all mammals except the Monotremes the trigeminal nerve is distributed by the supra-orbital, infra-orbital, and mental foramina in relation to the supra-orbital, mystacial, and mental vibrissæ which are receptor organs for the nerve. The Monotremes lack vibrissæ—according to Huber they never possessed them—and the foramina are quite otherwise arranged. There are no less than fourteen of these apertures for the peripheral distribution of the fifth nerve, ordered similarly in both. Those in *Ornithorhynchus* are much the larger, in keeping with the greater size of the nerve. The specialized sensory nerve-endings in the snout of *Ornithorhynchus*—the " push-rods " of Wilson and Martin (1894) and Poulton (1894)—contribute to the sensitivity of the delicate bill whose receptive surface is further extended by the shield-like flaps at its base. In *Echidna* the snout is smooth but hard, and no such specialized sensory receptors have been described, but the

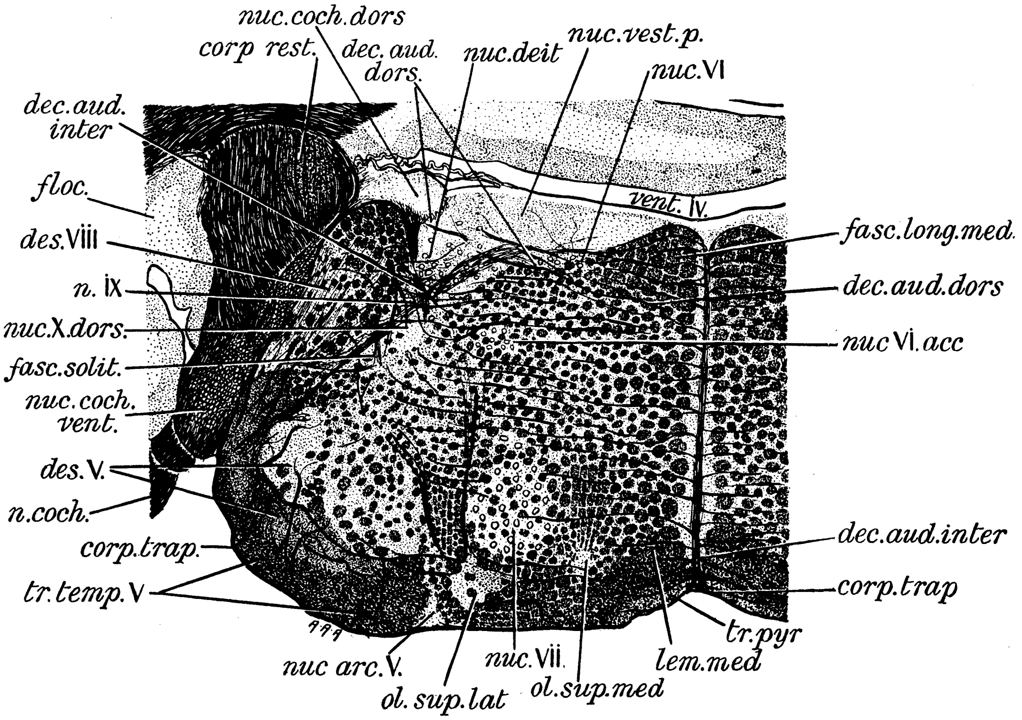

Fig. 10—Section from the Ziehen series. × 10. This lies just anterior to the level of the last and shows the nucleus arcuatus trigemini joining the lateral part of the superior olive. The three auditory decussations can be seen. In this series the tractus temporo-trigeminalis is well differentiated.

hypertrophy of the trigeminal nerve leaves little room for doubt that the snout is extremely sensitive. The only animals which can rival the Monotremes in development of the trigeminal nerve are the extinct Zeuglodonts described by DART (1923).

The fifth nerve enters the brain at the anterior border of the pons lateral to the rostrum, fig. 3. In these specimens the motor root was cut off. After entrance, fig. 13, the fibres are variously distributed. The great majority immediately turn caudally as the descending root, many pass directly to the cerebellum, others reach the pons, either to end among the nuclei or to cross with the pontine fibres. Many root-fibres pass with the lateral lemniscus to the tectum mesencephali, especially to the superior colliculus, while some ascend along the brachium conjunctivum to the cerebellum.

The chief sensory nucleus is very large and incompletely divided into medial and lateral parts, of which the lateral extends some way among the extracerebral root-fibres. The nucleus of the descending root is a caudal extension of the chief sensory nucleus. It accompanies the root through the medulla oblongata, and in the cord passes to the substantia gelatinosa ROLANDI in the usual manner. The secondary fibres from the chief sensory nucleus are mostly directed to the opposite medial lemniscus, and the massive trigeminal decussation is a feature of sections through this part of the brain-stem, fig. 13. Other secondary fibres pass dorsally before turning towards the mid-line. These form the dorsal secondary reflex path of WALLENBERG (1905), and can be seen to come into close association with the medial longitudinal fasciculi. The chief sensory nucleus also gives fibres to the pons and cerebellum. Few, if any, secondary fibres pass from the descending root and nucleus to the medial lemniscus, the only obvious contribution to this is from the chief sensory nucleus. This contribution is so massive that the medial lemniscus is doubled in size.

The descending root and its nucleus effect large and important connections with other structures in the medulla oblongata. Not only are they intimately related to the pons, but they also send many fibres to the corpus trapezoideum (as SCHEPMAN, 1918, noted) and to the external arcuate fibre system. Thus trigeminal impulses have yet another path by which to reach the cerebellum. The descending root is also closely related to the tractus temporo-trigeminalis, the nucleus arcuatus trigemini and the superior olive, the inferior olives and the lateral reticular nucleus.

The motor nucleus is much larger than would be expected in an animal whose jaw musculature is practically atrophied, fig. 13. Its cells equal in size those of the seventh nucleus and its function is difficult to estimate. The motor root-fibres pass ventrally and emerge medial to the entering sensory root.

The mesencephalic nucleus is also large. It is confined to the tectum mesencephali in which it extends from the posterior commissure to the anterior medullary velum. It comprises a median division and two lateral extensions, fig. 15. The median division consists of a column of cells lying in the mid-line dorsal to the aqueduct. In the hæmatoxylin series it bulged the ependyma in the roof of the aqueduct in places so that the cells depended like bunches of grapes. The lateral divisions extend as far laterally as the apex of the arc of the mesencephalic root. The cells of the lateral division are scattered, but they reach more frontally than those of the median group, which is contrary to the description of VAN VALKENBURG (1911). The root is quite large and the fibres collect to form a thick mass which borders the central grey matter and runs ventrally and caudally. The fibres join the motor root for the most part, but some appear to pass to the sensory.

The trigeminal nerve is very greatly hypertrophied, and it is doubtful if any part of the brain escapes its influence. The connections in the medulla oblongata, especially with the co-ordinating mechanism, are very extensive, and it will be shown later that the cerebellum, mid-brain, thalamus, and fore-brain are equally dependent upon the trigeminal apparatus. Some aspects of the question merit further consideration.

According to WALLENBERG (1905) the dorsal secondary reflex path serves to connect the sensory fifth nucleus with various motor nuclei, and especially the third. Both he and KAPPERS (1920) regard this as a purely reflex path. WINKLER (1921, *a*), who has studied this tract in an elaborate experimental investigation, states that it extends some way caudally into the medulla, and that frontally it constitutes a dorsal trigeminal lemniscus which is distributed mainly to the thalamus. HUBER and CROSBY (1929, *a*) also regard the tract as lemniscal in nature. Taking into account the facts that the fifth nerve already possesses a very good thalamic connection in the medial lemniscus, and that the dorsal secondary path closely accompanies the medial longtitudinal fasciculus and is related like this to the motor nuclei, it appears more likely that it is a reflex co-ordination pathway exactly analogous to the medial longitudinal fasciculus but related more intimately to the fifth nerve than to the eighth.

According to VAN VALKENBURG (1911) the mesencephalic nucleus of the fifth nerve in *Echidna* is very like that in sub-mammalia in its almost exclusively mid-line distribution. The marsupials exhibit a condition intermediate between that of *Echidna* and the higher mammals in the better development of the lateral extensions. In higher mammals the mid-line accumulation tends to disappear. In the sections examined—five series in all—the lateral extensions in *Echidna* are better developed than VAN VALKENBURG describes, and this animal shows a distinct advance upon the Sauropsidan condition as he figures it.

The mesencephalic nucleus and root of the fifth nerve are generally considered as mainly associated with proprioceptive sensibility of jaw musculature—see, for example, WILLEMS (1911), MAY and HORSLEY (1910), and ALLEN (1919) ; others assign to it a similar function for the ocular muscles. In *Echidna* the jaw musculature is atrophied and the eyes of little functional importance. On the other hand, the fifth motor and oculomotor nuclei are developed much beyond their presumed requirements. There is probably some relation between the size of these nuclei and the development of the mesencephalic nucleus of the fifth nerve, but their ultimate function is extremely obscure.

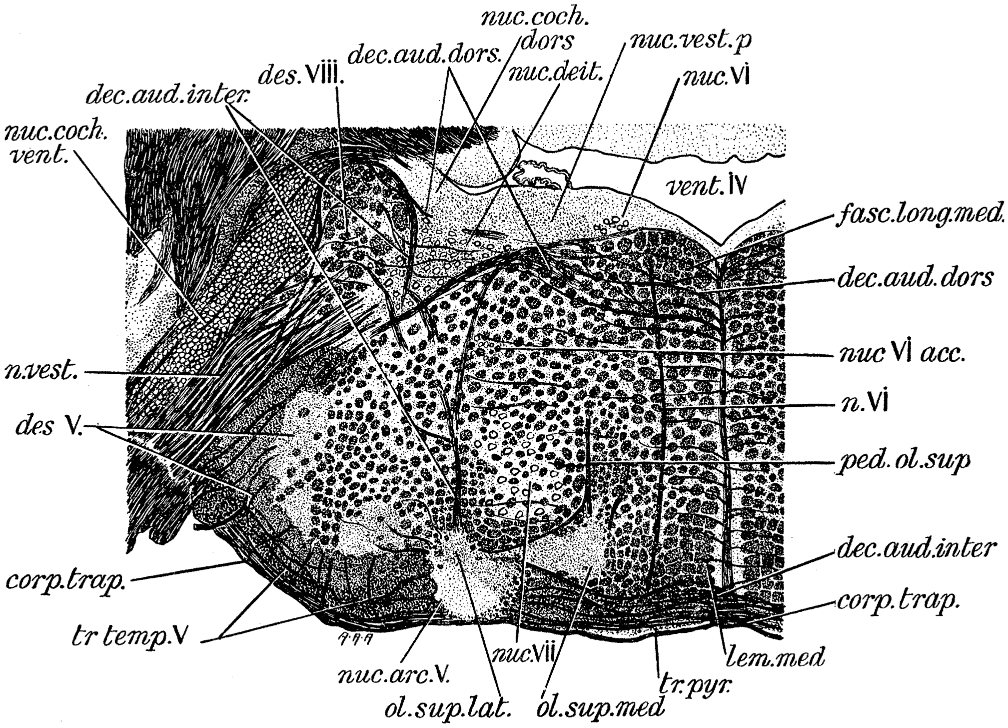

FIG. 11—Also from the ZIEHEN series. × 10. This shows the entrance of the vestibular nerve. The two parts of the superior olive are continuous ; both contribute to the peduncle, and both are intimately related to the descending root of the fifth nerve and the tractus temporo-trigeminalis. The seventh nerve is beginning to send off its dorsal extension ; above that lies the accessory sixth nucleus.

The Tractus Temporo-trigeminalis.—In his original description KÖLLIKER named this tract the " Zonalbündel " from the marginal relation which it bears to the descending root of the fifth nerve, fig. 10 (*tr.temp.v*). He described it as arising from the lateral funiculus of the cord and passing frontally with the trigeminal nerve. He thought that it passed to the cerebral peduncle, the medial lemniscus, and the tegmentum after decussation in the pons, and regarded the tract as an ascending one although unable to indicate its possible function. ZIEHEN's description differs from that of KÖLLIKER only in that he regarded the tract as descending. FUSE's (1926,*f*) description adds nothing to that of the two previous writers but, as already mentioned, he looked upon the tract as an aberrant pyramidal tract. Since the pyramids have been shown to follow the usual mammalian course, this opinion is quite untenable.

In the medulla oblongata the tractus temporo-trigeminalis lies around the medial and ventral aspects of the descending fifth root, fig. 10. The fibres are more numerous on the medial side of this root. When it is followed to the cord the tract passes into the lateral funiculus ; in a frontal direction it can be traced as far as the general decussation in the pons, fig. 12. To elucidate the further course of this tract it is necessary to follow the cerebral peduncles into the pons from above. As mentioned before, the pyramids lie at the medial border of the peduncles and are the first to enter the rostrum. Then the remaining fibres become enclosed by the rapidly widening pons in order from the most medial to the most lateral. The first fibres to enter soon break up amongst the pontine nuclei and give rise to secondary fibres which cross to the opposite brachium pontis, fig. 14. The last fibres to be included do not, however, break up in the same manner but appear to cross without the intermediation of the pontine cells. The last fibres arise from the temporal area of the cerebral hemisphere (area 4 of Schuster, 1910) and lie at the lateral border of the basis pedunculi. When they cross in the pons they cut off a projection of pontine cells which Ziehen called the nucleus lanciniatus. Then the fibres collect at the medial border of the newly-formed descending fifth root, fig. 12.

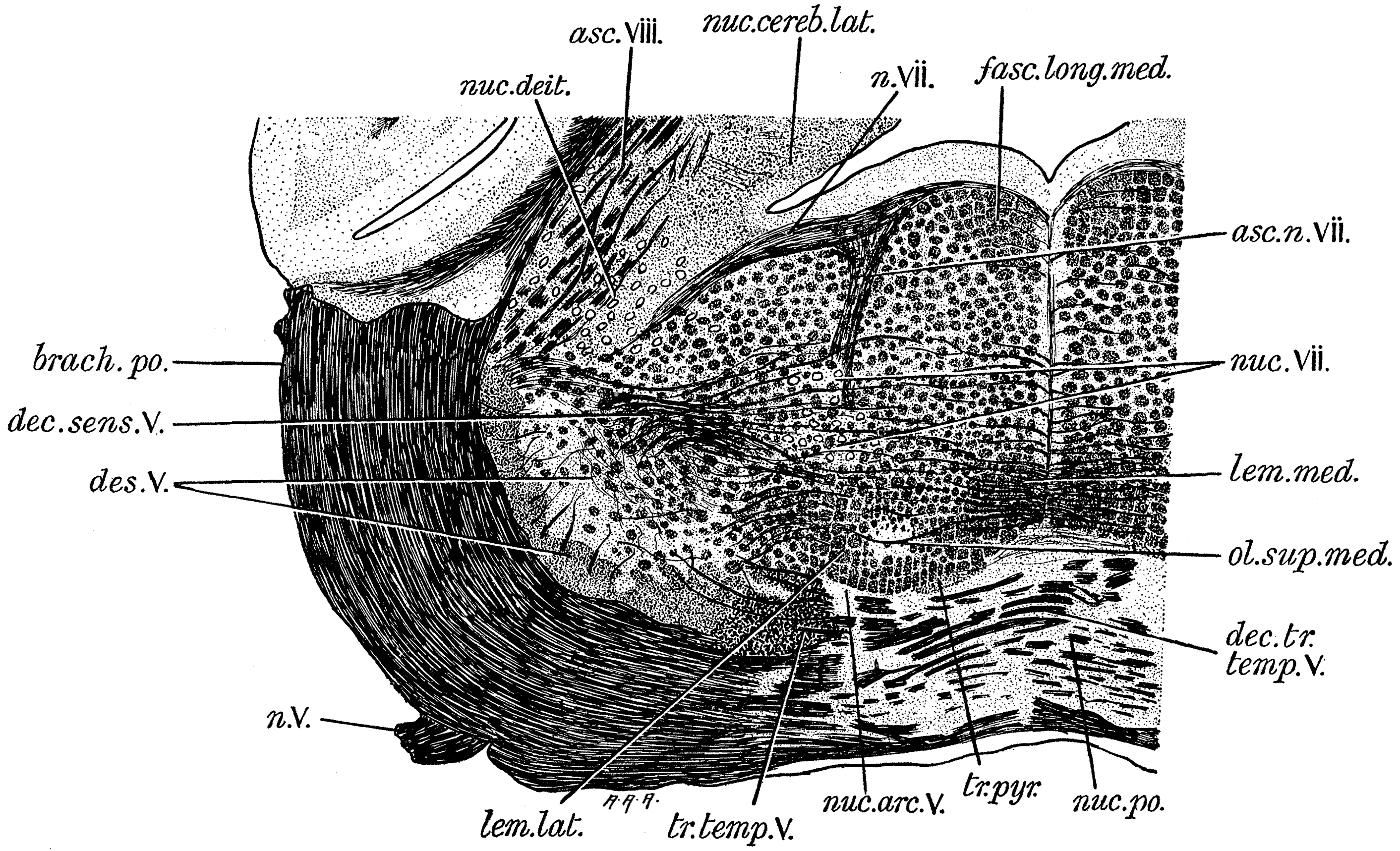

Fig. 12—Section through the crus pontis. × 10. This shows the tractus temporo-trigeminalis crossing to join the medial border of the descending root of the fifth nerve. The lateral part of the superior olive is joining the pontine nuclear mass ; the medial portion persists as the ventral nucleus of the lateral lemniscus. Note that many trigeminal fibres pass to the pons.

The tractus temporo-trigeminalis thus arises from the temporal region in the cortex, passes caudally in the lateral border of the cerebral peduncle and crosses in the pons to reach the medial side of the opposite descending fifth root. In its course through the medulla oblongata it is accompanied on its medial side by the nucleus arcuatus trigemini which was formed from the cut-off nucleus lanciniatus of the pons.

Kölliker, Ziehen, and Fuse all regarded the crossing in the pons as a total decussation. Certainly the majority of the fibres appear to cross directly, but some, at least, seem to end in relation to the pontine cells. Degeneration experiments are required to settle this point.

Kölliker and Ziehen both described the fibres of the tractus temporo-trigeminalis as staining more darkly than those of the descending root of the fifth nerve. According to Ziehen this is due to the greater thickness of the medullary sheaths ; the same author states that the tract myelinates later than the descending root. In the Weigert-Pal Carmine series this differentiation was not obvious, but in the Ziehen series, figs. 10 and 11, a sharp distinction could be drawn.

In the medulla oblongata there is a constant interchange of fibres with the descending root and nucleus of the fifth nerve ; the tract is also intimately related to the arcuate fibre system both directly, and through the agency of the nucleus arcuatus trigemini, fig. 8. Thus it affords an opportunity for the interrelation of cerebral, trigeminal, and vestibular impulses, and for the transmission of the resultant to the cerebellum. The disposition of this tract is strongly reminiscent of that of the usual cortico-pontine and cortico-arcuate fibres. It probably ends partly in the pons to send impulses to the cerebellum, it certainly sends many fibres to the corpus restiforme *via* the arcuate fibre system. There appears to be a close analogy between the two mechanisms : the cortico-pontine and cortico-arcuate fibres subservient to the vestibular interests of the medulla oblongata and cerebellum, the temporo-trigeminal to the trigeminal.

It is to be expected that the important trigeminal apparatus will dominate all cerebral functions and especially those of such biological significance as balance and the reception of vibratory impulses. It is not at all surprising, therefore, to discover that the cerebral hemispheres themselves have become harnessed to this trigemino-vestibular couple to provide a moiety of conscious direction. The great development of the trigeminal and spinal sensory systems, and their close association with the vestibular apparatus, provides an excellent anatomical opportunity for the exercise of that " tactile sense of vibrations " which Wood Jones (1923) describes as extraordinary. Further, the presence of such a tract in *Echidna*, and its absence in *Ornithorhynchus* (Kölliker, Ziehen), may supply a partial explanation for the much greater size of the non-olfactory pallium in the former. It shows an advance upon the condition in *Ornithorhynchus* since it provides a mechanism for rapid cortical reaction to trigeminal as well as to vestibular impressions.

The Inferior Olive—The olive has been described by Kooy (1916), and this account confirms his observations. The outer part of the olive consists of a column of cells horse-shoe shaped in transverse section with the hilum directed ventrally, fig. 8. Within this lies a cylindrical rod of cells continuous at various levels with either of the limbs of the outer arch. The nucleus extends from the caudal border of the medulla oblongata almost to the superior olive, but the inner rod of cells is deficient at both extremities. The cells of both portions are small and closely packed.

The inferior olive receives numerous fibres from the gracile and cuneate nuclei and from the descending root of the vestibular nerve. These fibres appear to be both crossed and uncrossed. Many external and internal arcuate fibres are given off to the opposite corpus restiforme. The caudal part of the medial lemniscus lies in and around the inferior olive. The emerging root-fibres of the twelfth nerve pass between the olive and the lateral reticular nucleus which is, however, continuous in places with the olive. The olive is also continuous to some extent with the arcuate nucleus.

Kooy states that the dorso-lateral part of the inferior olive in *Echidna* is the homologue of the dorsal accessory olive in higher mammals, the medial part that of the medial accessory olive. The remainder represents the principal inferior olive.

The Lateral Reticular Nucleus—This was described by Kölliker as the medial nucleus of the lateral funiculus. He regarded it as a lobe of the inferior olive, an opinion which Ziehen, Kooy, and Fuse (1926, *d*) do not share. It is a large reticular mass of cells, fig. 8, incompletely separated from the inferior olive by the root-fibres of the hypoglossal nerve. Its cells resemble very closely those of the inferior olive and the arcuate nucleus, and, although its fibre connections are obscure, it appears to be in close functional harmony with its two neighbours.

The Arcuate Nuclei—These are large masses of cells lying among the external arcuate fibres in close relation to the hypoglossal root, fig. 8. Fuse (1926, *a*) has described them very briefly, chiefly to emphasize the necessity of not confusing them with the inferior olives. The arcuate nuclei are continuous in places with the olives, but there is little possibility of mistaking such discrete cell masses for other than what they are.

The Nucleus Arcuatus Trigemini—Kölliker described this mass as the lateral nucleus of the lateral funiculus, Fuse (1926, *d*) as the nucleus of the " Zonalbündel." Since it is associated with the trigeminal apparatus on the one hand, and with the arcuate fibre system on the other, the above title appears to be more appropriate. As described above, the decussation of the tractus temporo-trigeminalis in the pons cuts off the nucleus lanciniatus from the rest of the pontine nuclear mass, fig. 12. More caudally this nucleus forms the lateral part of the superior olive, figs. 10 and 11. Here it is divisible into a lateral light-stained part and a medial darker portion. Behind the level of the auditory decussations only the light stained part persists. This lies against the medial side of the tractus temporo-trigeminalis, figs. 9, 8, and 7 (*nuc.arc.v*), where it forms a cell column which is usually continuous, but which may—as Fuse points out—be interrupted at one or more places. The nucleus exchanges fibres with the tractus temporo-trigeminalis and the descending root and nucleus of the fifth nerve. It also receives dorsal and ventral internal arcuate fibres from both sides and is intimately related to the external arcuate fibre system.

The Arcuate Fibre Systems—The external arcuate fibres form a continuous layer over the ventral surface of the medulla oblongata. In places they are gathered into local accumulations, fig. 3. The fibres arise from the inferior olives, the gracile and cuneate nuclei and the descending root of the opposite vestibular nerve. It is important to note that the external arcuate fibre system receives a big contribution from the descending fifth root and from the tractus temporo-trigeminalis, fig. 8. The nucleus arcuatus trigemini serves to inter-relate cerebral, trigeminal, and vestibular impulses and transmit them by the external arcuate fibres to the cerebellum. The remaining arcuate nuclei lie among the external arcuate fibres and act as mediators of cerebral and other impulses. The fibres join the corpus restiforme to reach the cerebellum ; on the way many pass through the tractus temporo-trigeminalis and the descending root of the fifth nerve, fig. 8.

The internal arcuate fibres can be divided into dorsal and ventral sets. The dorsal arise from the descending vestibular root and pass medially to the medial longitudinal fasciculi. Here many end, but a few appear to pass beyond and reach the nucleus arcuatus trigemini of the other side, fig. 8. The ventral internal arcuate fibres arise from the gracile and cuneate nuclei and from the descending vestibular root. The former pass chiefly to the opposite inferior olive, the latter to the nucleus arcuatus trigemini of the same side. A few emerge as external arcuate fibres. Other ventral internal arcuate fibres run in the reverse direction from the inferior olive to the opposite corpus restiforme.

The Corpus Restiforme—This arises in the usual manner around a core of dorsal spino-cerebellar fibres, fig. 8. The body is enlarged by the addition of external and internal arcuate fibres and of dorsal external arcuate fibres from the gracile and cuneate nuclei of the same side. It gains fibres from the gracile and cuneate nuclei of both sides (but chiefly from the opposite side), the inferior olive, the arcuate nuclei, the nucleus arcuatus trigemini, the spinal fifth root, the tractus temporo-trigeminalis, the descending vestibular root, and probably from the nucleus reticularis lateralis.

The whole fibre mass enters the cerebellum at a very acute angle. So abrupt is the ascent that the restiform body lies almost entirely dorsal to the cochlear nerve, and its pressure completely divides the posterior part of the ventral cochlear nucleus, fig. 9. In nearly all mammals the restiform body passes ventral to the cochlear nerve and its ventral nucleus before ascending to the cerebellum. In *Didelphys* (STOKES) and *Macropus* (FUSE) the body passes through the cochlear nerve, dividing the posterior part of the ventral nucleus as in *Echidna.*

The Eighth Nerve—The vestibular division constitutes about two-thirds of the bulk of the eighth nerve and is distinguished by its coarse texture. It enters the brain immediately at the posterior border of the pons, ventro-medial and anterior to the cochlear division, fig. 1. Many of its fibres enter the cerebellum at once, fig. 11, a few join the corpus trapezoideum (in contrast to the cochlear nerve), but the majority enter the ascending, and especially the descending, vestibular roots. A few fibres enter the principal vestibular nucleus, and DIETER's nucleus is so closely related to the descending root that it must receive many. A few vestibular fibres run directly to the three acoustic decussations and a very few appear to join the descending root and nucleus of the fifth nerve, fig. 11.

The ascending and descending vestibular roots and their nuclei form a continuous system from the anterior limit of the pons to the posterior border of the medulla oblongata. The ascending root and the nucleus of BECHTEREW—which WINKLER (1921, *b*) has shown to be an anterior continuation of the nucleus of the descending root—pass dorsally into the wall of the fourth ventricle where the fibres gradually end in the cerebellar nuclei and the cerebellum itself, fig. 12. The descending root is very large. It receives a few cochlear fibres and descends with its nucleus to the caudal limit of the medulla oblongata and is lost at the medial side of the gracile-cuneate mass, fig. 8.

Throughout their combined course the roots give off large numbers of fibres and are thus gradually dissipated. These fibres form two chief sets. The smaller comprises the dorsal internal arcuate fibres, many of which end in the medial longitudinal fasciculi. A few pass beyond and appear to reach the opposite nucleus arcuatus trigemini, fig. 8. The larger group constitutes the ventral internal arcuate fibres. Some of these pass directly ventrally to the nucleus arcuatus trigemini of the same side ; the remainder reach the opposite inferior olive to be related to the opposite internal and external arcuate systems.

At the level of entrance of the vestibular nerve the same three decussations exist, but are much larger, and the nuclear masses in relation to them receive different names. The nucleus arcuatus trigemini becomes included in the lateral part of the superior olive, the inferior olive gives way to the medial part of the superior olive, and the arcuate nuclei are represented by the nucleus of the corpus trapezoideum.

Anterior to the level of entrance of the eighth nerve dorsal internal arcuate fibres are given off from the ascending vestibular root. STOKES (1911) described these as the decussation of the nucleus of BECHTEREW, but WINKLER (1921, *b*) has shown that the majority end in the medial longitudinal fasciculi.

DEITERS' nucleus has been described by FUSE (1926, *c*), who divides it into five cell groups. The middle group lies at the posterior level of the vestibular nerve between the dorsal and ventral parts of MEYNERT'S I.A.K. field, and adjoining the ventral ganglion. The inter- or intra-medullary group lies slightly anterior to the middle group between the vestibular nerve fibres. The ventro-medial group lies in the ventral I.A.K. field. These three groups join anterior to the vestibular nerve and can be differentiated no longer. The triangular group overlaps the lateral part of the principal vestibular nucleus. The dorso-medial group is scattered amongst the fibres of the I.A.K. field, and anterior to this cannot be distinguished from the other groups. Such an elaborate analysis is not attempted here, but it can be seen, figs. 10, 11, 12, and 13, that the large cells of DEITERS' nucleus are distributed over a wide area whose limits correspond approximately to those of FUSE'S description.

The principal or triangular nucleus is the direct anterior continuation of the nucleus intercalatus, fig. 10. It is composed of a medial small-celled part and a lateral larger-celled portion. According to SCHEPMAN (1918) these correspond respectively to the nuclei piriformis and vestibulo-cerebellosus of birds. The connections of this nucleus are, despite its large size, difficult to determine. It receives some vestibular root-fibres and sends some fibres to the medial longitudinal fasciculi.

Echidna is the most primitive mammal to show any advance upon the birds in the evolution of the labyrinth. Whereas in *Ornithorhynchus* the whole labyrinth is typically avian, in *Echidna*, according to GRAY, A. A. (1908), the vestibule has advanced well towards the mammalian type and the cochlea has enlarged. But it retains a lagena at the tip and still falls short of one complete turn. The central connections of the cochlear nerve reflect accurately the evolution of the cochlea for, while they are distributed in a typically mammalian fashion, they are so scanty they they form a mere skeleton framework for the subsequent great development and can be readily distinguished from the much more massive vestibular connections.

The cochlear nerve enters the brain dorso-lateral and posterior to the vestibular division. The fibres come into immediate relation with the ventral cochlear nucleus which is here partly divided by the pressure of the corpus restiforme, fig. 9. When relieved of this pressure anteriorly the two divisions become continuous, fig. 11. An appreciable number of the entering fibres pass directly to the corpus restiforme and cerebellum, fig. 9, many end in the ventral cochlear nucleus, and the remainder run dorsally and medially, ventro-medial to the restiforme body. No direct cochlear fibres could be seen to pass to the corpus trapezoideum, although SCHEPMAN describes such. Some of the fibres end in the dorsal cochlear nucleus, and a few—which probably come from the saccule and posterior ampulla—join the descending vestibular root. Many fibres pass directly to the dorsal and intermediate auditory decussations.

The ventral cochlear nucleus is well developed and comprises large multangular cells, fig. 9. Many cochlear fibres pass to the nucleus. Some end there, others pass on to the dorsal nucleus or beyond. Secondary fibres pass to the corpus restiforme and cerebellum, others to the auditory decussations. Those passing to the corpus trapezoideum are few and difficult to find, fig. 10.

The dorsal cochlear nucleus is much smaller than the ventral. It lies at the lateral angle of the fourth ventricle to form a low tuberculum acusticum, fig. 10. Posteriorly it extends slightly caudal to the ventral nucleus ; anteriorly it falls far short of this. The cells of the dorsal nucleus are small. The nucleus receives cochlear root-fibres and gives secondary fibres to the cerebellum and the auditory decussations.

It is now possible to consider the auditory decussations. There are three : the corpus trapezoideum, the intermediate decussation of HELD, and the dorsal decussation of VON MONAKOW.

The corpus trapezoideum in *Echidna* is small and cannot be recognized from the exterior. It receives fibres directly from the vestibular nerve, but none, so far as repeated examination would reveal, from the cochlear nerve. A very few secondary fibres pass from the ventral cochlear nucleus to the trapezoid body, but these are so scanty that they may be readily overlooked, fig. 10. A relatively large number passes from the descending root and nucleus of the fifth nerve to the corpus trapezoideum, either directly, or after synapse in the lateral part of the superior olive ; and this, as has been shown, comprises, in part, the nucleus arcuatus trigemini. The remainder of the fibres in the diminutive corpus trapezoideum—and these form the great majority—pass to the corpus restiforme and the cerebellum. That is, the largest part of the corpus trapezoideum in *Echidna* is composed of external arcuate fibres. Posteriorly the corpus trapezoideum merges imperceptibly in the remainder of the external arcuate fibres ; anteriorly it is continuous with the pons.

It has been shown that the pons and its nucleus receive many contributions from the fifth nerve. The corpus trapezoideum acquires many trigeminal fibres, as SCHEPMAN also noticed, and it has been emphasized repeatedly that trigeminal fibres pass in large numbers to the external arcuate system. HUBER and CROSBY (1926) have shown that trigeminal fibres form the primitive basis of all external arcuate fibres, and DART (1923) that the cerebellum has a trigeminal as well as vestibular foundation. In *Ornithorhynchus*—where there is no corpus trapezoideum—the external arcuate fibres are continuous with the pons, which is so poorly developed that it is scarcely distinguishable from them. (This is clearly demonstrated in a series of *Ornithorhynchus* sections in the Department of Anatomy at University College, London.) Thus it seems clear that the pons and external arcuate fibre system form one continuous series of fibres founded on a primitive trigeminal basis. With the advent of cortical connections more and more eighth neuromere (rhombic lip) elements were added to the system and so increased that they obscured the trigeminal foundation. The greatest accumulation of these elements is in the immediate neighbourhood of the cerebellum itself—in the pons ; the remainder scatter caudally in association with trigeminal fibres as arcuate nuclei and external arcuate fibres. The purpose of the pontine-arcuate system is simply the mediation of cortico-cerebellar impulses.

When the cochlea evolved from the labyrinth it employed the existing vestibular connections within the brain, and when it attained mammalian status a corpus trapezoideum appeared. The corpus trapezoideum in *Echidna* is so rudimentary that it reveals its primitive vestibular and primary trigeminal origin, for it consists almost entirely of external arcuate fibres which include a large trigeminal element. (It is of interest to note that STOKES describes fibres passing from the corpus trapezoideum to the corpus restiforme and cerebellum in *Didelphys*, so that in this marsupial external arcuate fibres can be detected in the trapezoid body.) It is possible to assert that the corpus trapezoideum is merely a localized infiltration of the external arcuate fibre system by cochlear fibres, and that the pons, corpus trapezoideum, and external arcuate fibres constitute one continuous system. In higher mammals the sudden great increase of cochlear elements has almost completely obscured the original trigeminal and vestibular connection. But vestibular fibres can always be found in the corpus trapezoideum, as INGVAR (1918), SCHEPMAN (1918), and WINKLER (1921, *b*) have shown, and the poor cochlear development in *Echidna*

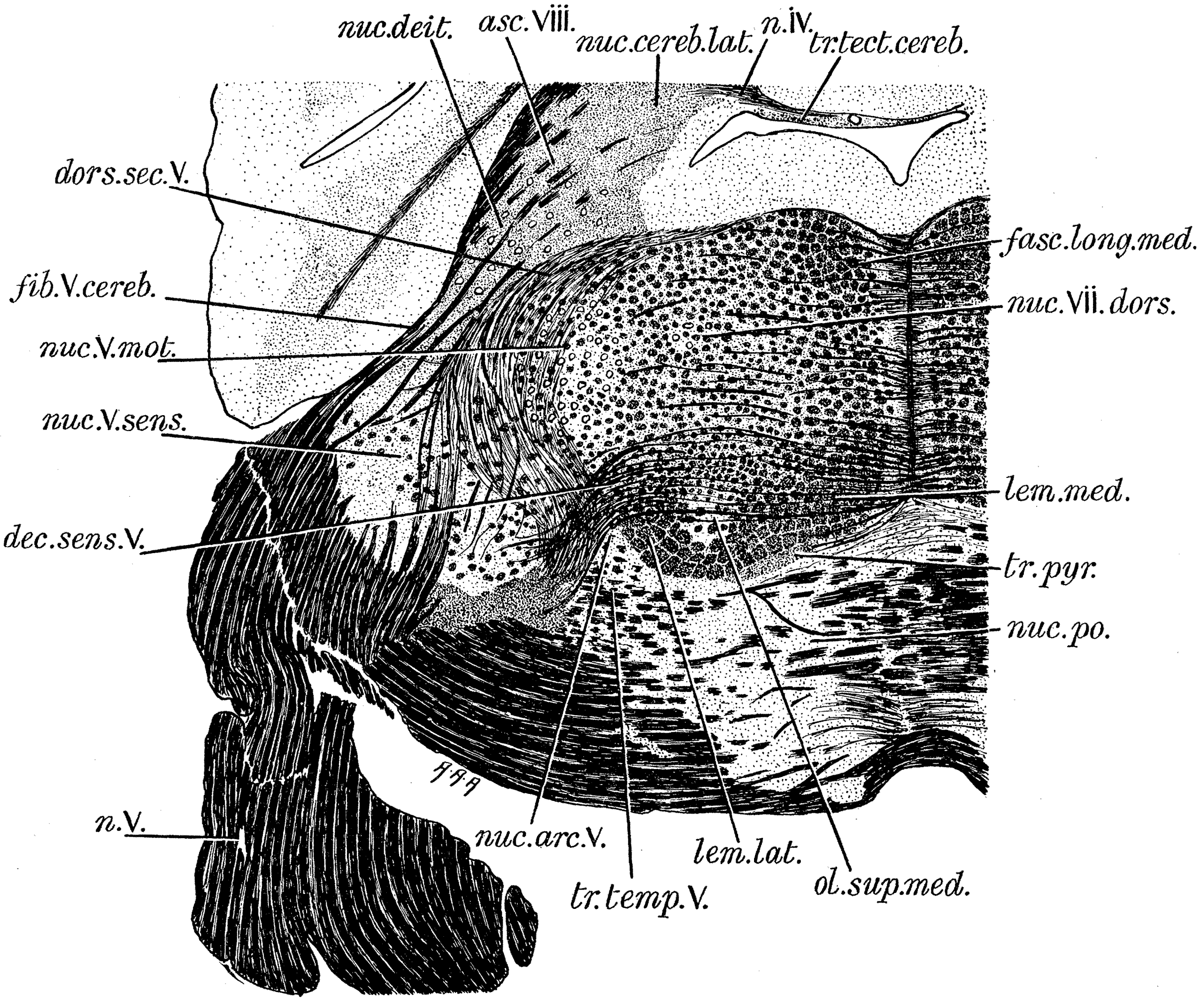

FIG. 13—At the level of entrance of the fifth nerve. × 10. Dorsal secondary reflex fibres form a large bundle passing towards the medial longitudinal fasciculus. Many trigeminal fibres reach the cerebellum and pons. The fifth motor nucleus is large and just medial to it lies the anterior tip of the dorsal extension of the seventh nucleus.

renders them conspicuous. This, added to the great hypertrophy of the trigeminal apparatus, emphasizes the trigeminal origin of all these systems.

The superior olive has been described by FUSE (1926, *d*). It comprises medial and lateral parts. Caudal to the commencement of the lateral lemniscus the two are continuous, fig. 11. The nucleus arcuatus trigemini lies within the lateral portion. As the lateral lemniscus forms it expands between the two parts of the olive, and these pass forwards on its medial and lateral borders, fig. 12. Towards the anterior part of the pons the lateral part joins the nucleus lanciniatus of ZIEHEN which projects between the lateral lemniscus and the descending fifth root, and thus becomes continuous with the pontine nuclei. The medial part continues forwards on the medial side to become the ventral nucleus of the lateral lemniscus, fig. 14.

The greater part of the superior olive is of rhombic lip origin. There is some reason to believe that part—the nucleus arcuatus trigemini—may be of fifth neuromere origin. These two portions, then, are strictly comparable with the inferior olive (rhombic lip) and more caudal nucleus arcuatus trigemini respectively. Frontally they are represented in rhombic lip and trigeminal elements in the pontine nuclear mass. As the cochlear connections in the medulla oblongata increase, the superior olive hypertrophies in accordance. In higher mammals it becomes multilobular and produces an accessory olive.

In a few sections a small collection of cells can be found lying amongst the fibres of the elementary corpus trapezoideum. KÖLLIKER described this as the nucleus of the corpus trapezoideum. Since the corpus trapezoideum is chiefly composed of external arcuate fibres, this must be considered an arcuate nucleus. But there is little doubt that it represents the nucleus of the corpus trapezoideum of higher mammals.

It has been stated that very few cochlear fibres join the corpus trapezoideum, the majority pass dorsally and medially between the corpus restiforme and the descending vestibular root, fig. 11. They turn medially, dorsal to this root, and most bend acutely ventrally to reach the lateral part of the superior olive of the same side. From the olive secondary fibres arise which cross the mid-line dorsal to the corpus trapezoideum. This constitutes the intermediate decussation of HELD. The number of cochlear fibres in this decussation is not great, for it is seen to be composed largely of fibres from the descending vestibular root. More caudally the same decussation was found to be composed entirely of vestibular connections which were described as ventral internal arcuate fibres. At the level of entrance of the eighth nerve the ventral internal arcuate fibres have become permeated by cochlear elements to form the intermediate decussation of HELD.

A very few cochlear fibres from the area dorsal to the descending vestibular root pass directly medially with vestibular fibres towards the medial longitudinal fasciculi. Some cross to join the opposite superior olive. This is the dorsal decussation of VON MONAKOW—the striæ medullares acusticæ. It is clear that the dorsal decussation is no more than a permeation of the dorsal internal arcuate fibres by cochlear fibres. In *Echidna* this decussation is still chiefly vestibular, very few cochlear fibres enter into its composition.

In *Ornithorhynchus* KÖLLIKER thought he could distinguish a corpus trapezoideum. ZIEHEN, after much hesitation, confirmed this. HINES, however, gives a different description. She says (p. 218), " But unlike the findings of both SCHEPMAN (1918), for *Echidna*, and STOKES (1912), for the opossum, the fibres of the *corpus trapezoideum* pass *medial and dorsal to the sensory nucleus of the trigeminus rather than lateral and ventral to it.*" (My italics.) Clearly she is describing the intermediate decussation of HELD and not the corpus trapezoideum, for this always passes lateral and ventral to the descending fifth root. Some *Ornithorhynchus* sections which I have examined confirm that there is no corpus trapezoideum, and that the auditory decussations resemble those in the Sauropsida where there is likewise no corpus trapezoideum.

This is to be expected in view of the fact that the labyrinth in *Ornithorhynchus* shows little or no advance upon that of reptiles and birds. In the Sauropsida the chief auditory crossing is the intermediate decussation of HELD, as can be seen in the papers by SCHEPMAN (1918), KAPPERS (1921), WINKLER (1918), and HUBER and CROSBY (1926). HELD (1893) demonstrated that it myelinates at an earlier stage than the others and is to be regarded as phylogenetically older. STOKES (1911) and FUSE (1926, *c*) have shown that in marsupials, although the corpus trapezoideum is massive, the intermediate decussation still conveys a large number of cochlear fibres.

The intermediate decussation is, then, the most primitive of the auditory crossings. It is practically the sole method of decussation in the Sauropsida and in *Ornithorhynchus*, and in *Echidna* still conveys the greatest number of fibres. In higher mammals it increases in size but is rapidly surpassed by the corpus trapezoideum.

Very few cochlear fibres join the dorsal decussation. In *Echidna* this is still chiefly vestibular. WINKLER, VON MONAKOW, and others consider the striæ medullares the main path of cochlear decussation in higher mammals. POLJAK (1926) has recently denied this, and has shown that in bats very few cochlear fibres cross in the dorsal decussation. The condition in *Echidna* and the marsupials supports his views. He quotes the opinion of CAJAL that the dorsal decussation is a reflex path, and there is, of course, no guarantee that the cochlear fibres crossing there convey auditory impulses, since fibres from the saccule and posterior ampulla join the cochlear nerve.

Thus the three auditory decussations have developed from the three primary vestibular decussations, just as the cochlea itself has evolved from the primitive labyrinth. These vestibular decussations are the external, and the dorsal and ventral internal arcuate fibre systems. The external arcuate fibres have, in turn, been imposed upon a primitive trigeminal system. At the level of entrance of the cochlear nerve the three systems are permeated by cochlear fibres. These invade first the ventral internal arcuate system to form the intermediate decussation of HELD, while a few cross with the dorsal internal arcuate fibres as the striæ medullares of VON MONAKOW. This is the condition found in the Sauropsida and in *Ornithorhynchus*. In *Echidna*, with its slight enlargement of the cochlea, a few cochlear fibres have invaded the external arcuate system to form a rudimentary corpus trapezoideum. In all higher mammals the majority of cochlear fibres employ this more direct path and a very conspicuous corpus trapezoideum results.

There is no fundamental distinction between vestibular and cochlear functions ; both are adapted to the reception of vibratory impulses, but the cochlea is especially attuned to their accurate analysis. Even fishes with no cochlea can respond to musical notes of low frequency, as KAPPERS (1921) has shown, and this author has well said that the vestibular apparatus represents the protopathic side of vibratory reception, the cochlear the epicritic. Such a permeation of a lower system by a higher is no novelty in cerebral evolution. The classical analogy is the invasion of the dorsal part of the hippocampal commissure by the corpus callosum, as ELLIOT SMITH (1897) demonstrated long ago ; and DART (1925) has shown that others can be found in the forebrain, thalamus, cerebellum, and spinal cord. It is, in fact, another example of his " infiltration theory."

The Pons

The pons in both Monotremes is peculiar in its wholly retro-trigeminal development. In *Echidna* it is a plump body, fig. 1, considerably larger than the corresponding organ in *Ornithorhynchus*. Anteriorly it projects forwards in the mid-line between the two trigeminal nerves as the rostrum of Elliot Smith (1895). This covers the caudal pole of the ganglion interpedunculare. The posterior border extends across the medulla oblongata with a slight posterior convexity. In the middle line is a shallow raphe. The sixth, seventh, and eighth nerves are attached to the medulla oblongata at the posterior border of the pons. The crura are massive bands which pass dorsally and posteriorly to enter the cerebellum.

In transverse section, fig. 12, the pons is found to consist essentially of a large nuclear mass encapsuled by a thin shell of fibres. The pontine decussation occurs in the anterior part of this mass, but is more of an incident than a marked feature. On each side a projection of pontine cells extends between the lateral lemniscus and the descending root of the fifth nerve to form the nucleus lanciniatus of Ziehen, fig. 13 (*nuc.arc.v*). It gives rise to the lateral part of the superior olive and the nucleus arcuatus trigemini. The pontine nuclear mass is composed of small, closely packed cells of exactly the same type as those of the superior olive, the nucleus of the corpus trapezoideum, the nucleus arcuatus trigemini, the inferior olive, the nucleus reticularis lateralis and the nuclei arcuati proper.

The mode of entry of the cerebral peduncles into the pons has already been described in the account of the tractus temporo-trigeminalis. Briefly, the pyramidal fibres enter the rostrum first and become related to the medial lemnisci. The next fibres to enter are the more laterally lying cortico-pontine and cortico-arcuate fibres. The cortico-pontine fibres end at once around the pontine cells, which give rise to secondary fibres, fig. 14. These cross the mid-line and collect at the periphery of the pons to form the fibrous capsule. In this they course laterally and posteriorly to reach the crus. The last fibres to enter the pons are those of the tractus temporo-trigeminalis. Some of these appear to end, but the majority cross directly to reach the medial border of the opposite descending fifth root, fig. 12.

The trigeminal nerve contributes a large number of fibres—both direct and secondary—to the pons. This confirms the observation of Wallenberg (1905) for the rabbit. In *Echidna* the proportion is probably greatly increased as the result of the general trigeminal hypertrophy. Some tectal fibres reach the pons. Posteriorly the pontine fibres are in continuity with those external arcuate fibres which are in process of forming a corpus trapezoideum.

The opinion has already been expressed that the pons represents a local hypertrophy of the external arcuate system. The large number of trigeminal fibres which enter its composition make it appear certain that the pons, like the arcuate system, has a trigeminal foundation. The pons represents the main part of the rhombic lip migration which has accumulated in close relation to the cerebellum, itself largely of rhombic lip origin.

The question remains : why does the pons lie posterior to the entrance of the fifth nerve ? Two explanations are possible : either the entrance of the nerve has been displaced forwards, or the pons betrays a purely retro-trigeminal development. The normal internal relations of the trigeminal system (allowing for its hypertrophy) render the former supposition untenable, the latter will be examined more closely after the description of the cerebellum.

The Cerebellum

In 1902 Elliot Smith said (p. 156), " In comparison with the corresponding organ in other mammals, the cerebellum in the Monotremes presents features so peculiar that no exact comparisons with that of other mammals can be instituted with any degree of certainty. The fissura prima (præclivalis of Human Anatomy) is apparently placed very far back, so that the greater part of the cerebellum, including the whole of the anterior and the greater part of the dorsal surface, corresponds to the anterior lobe of other mammals (the combined lobus centralis and lobus culminis of Human Anatomy). Thus the whole of the postclival region, which in the higher mammals becomes so greatly expanded that it forms the bulk of the organ, becomes relegated to the caudo-ventral region of the cerebellum and is a narrow insignificant strip which is expanded laterally only to a very slight degree." On p. 157 he says, " The cerebellum differs in a most marked manner from that of other mammals, and seems to be a highly specialized modification of the primitive mammalian type."

In her recent paper, Hines (1929) has discussed the cerebellum of the Monotremes at some length, and has tried to force a resemblance to that of the bird on the one hand and of the opossum on the other. To accomplish this she has quite arbitrarily identified the fissura prima as " ...... the deepest fissure towards the anterior pole of the cerebellum " (p. 225). There is no warrant for such homology ; as Elliot Smith (1899, *a*) says (p. 363), " this is the deepest fissure which crosses the mesial plane of the organ." It is a matter of no moment whether the fissure lies anteriorly or posteriorly, it is always the deepest. This is fully exemplified in the works of Elliot Smith (1903, *b*, *c*, and *d*), Bolk (1906), and Ingvar (1918), and the examination of a large series of cerebella from many animals reveals that the fissura prima is not only the most constant, but is always the deepest fissure. It is, indeed, the great depth of the fissure which serves as the essential basis for its identification.

The cerebellum in *Echidna* is large, but is compressed anteroposteriorly by the caudal projection of the cerebral hemispheres. The antero-superior surface extends between the diverging occipital poles in a wedge-like manner, fig. 2. The antero-inferior face is closely adapted to the contour of the posterior surface of the tectum mesencephali, fig. 1. Posteriorly the cerebellum is full and rounded and trilobular. The flocculi are represented by five or six small lobules closely pressed against the sides of the medulla oblongata. The surface is quite richly foliated.

In medial section, fig. 4, the fissura prima is at once revealed by its depth. It cuts the surface at the postero-superior angle and passes ventrally and anteriorly into the body of the organ. The same fissure was called the *fissura horizontalis magna* by ZIEHEN (1897, *a*), and the " deepest sulcus " by HINES. All the cerebellar tissue lying anterior to this fissure represents the lobus anterius of other animals, and it will be observed that the hypertrophy is restricted almost entirely to the culmen, the lingula and lobulus centralis are very little different from those of other mammals. In the culmen are several fissures, but two are of greater depth than the rest. They are labelled " a " and " b " in fig. 4. Fissure " b " corresponds to ZIEHEN's *sulcus cerebellaris posterior superior* and appears to be the same as that described by DE LANGE (1918) as the fissura prima, but his figures are so vague that this is not certain. ZIEHEN called fissure " a " the *sulcus cerebellaris anterior superior*, and it is this which HINES regards as the fissura prima. The examination of ten *Echidna* cerebella has shown that only the fissure described here as the fissura prima is constant in depth and position. The two deep fissures in the culmen, on the other hand, exhibit a considerable amount of variation, and are frequently represented by a single fissure which may bifurcate within the cerebellum. They are very unstable and could not possibly be mistaken for the fissura prima.

This median section is extraordinarily similar to median sections of the cerebellum of *Ornithorhynchus* as figured by ZIEHEN (1897, *a*), ELLIOT SMITH (1895), and HINES (1929). There can be no doubt that the fissure there, which corresponds almost exactly in position and shape with the fissura prima of the *Echidna* cerebellum, represents the fissura prima in *Ornithorhynchus*. Both animals thus fully justify ELLIOT SMITH's remarks concerning the great size of the lobus anterius.

Posterior to the fissura prima is the lobus medius, which is quite small. The deep fissura præpyramidalis defines the anterior limit of the large pyramid. Ventral and anterior to the pyramid is the fissura secunda, in size inferior only to the fissura prima. Anterior to the fissura secunda is the lobus posterius divided into uvula and nodule by the fissura uvulo-nodularis.

The nodule can be traced laterally in continuity with the flocculus, fig. 5. The uvula is entirely divorced from participation in the formation of the cerebellar hemispheres and offers no support for INGVAR's uncertainty as to whether or no it contributes to the paraflocculi. The large pyramid undergoes slight constriction in the copula pyramidis to expand laterally in the massive paraflocculus. These constitute the greatest part of the cerebellar hemispheres as DE LANGE has noted. The fissura præpyramidalis is continued laterally in the fissura parafloccularis which separates the paraflocculus from the rest of the lobus medius and joins the fissura prima in the lateral part of the hemisphere, fig. 2. Thus the non-parafloccular lobus medius forms a narrow strip of the cerebellum lying between the fissuræ prima and combined præpyramidalis and parafloccularis.

It does not even reach the lateral border of the cerebellum, for there it is limited by the junction of the fissura prima with the fissura parafloccularis.

The cortex of the cerebellum contains the usual molecular, Purkinje and granular layers. There are two cerebellar nuclei, medial and lateral. The lateral gives origin to the brachium conjunctivum and probably corresponds to the combined nuclei dentatus and globosus of higher mammals. The medial nucleus is much smaller and appears to represent the nuclei emboliformis and fastigii. Fibres enter the cerebellum in the corpus restiforme and the pons. Both convey numerous trigeminal contributions. In addition, fibres pass directly to the cerebellum from the entering trigeminal root, fig. 13, while others reach it *via* the brachium conjunctivum. The trigeminal nerve thus enters very largely into the formation of the cerebellum—a fact which HINES has noted for *Ornithorhynchus.* Ventral spino-cerebellar fibres reach the cerebellum along the brachium conjunctivum, and tecto-cerebellar fibres from the superior and inferior colliculi through the anterior medullary velum.

The outstanding features of the cerebellum of *Echidna* are the enormous hypertrophy of the lobus anterius and the paraflocculi, and the small size of the lobus medius. In marsupials and most other primitive mammals the lobus anterius is so small that it is often completely hidden from dorsal view by the large hood-like lobus medius. Thus the cerebellum in the Monotremes is the complete antithesis of that in all other primitive mammals. In higher mammals the increase in cortical connections has evoked a progressive expansion of the lobus medius which, in the higher Primates and Man, forms the major part of the total bulk of the cerebellum. But attention has been focussed so acutely upon the enlargement of the lobus medius that very little notice has been taken of the lobus anterius.

Examination of a series of cerebella quickly reveals that the lobus anterius has by no means lain dormant while the lobus medius developed. Had this been so, the lobus anterius, already diminutive in the marsupials, would have been pushed away to the base of the cerebellum by the expanding lobus medius, finally to be represented by an inconspicuous nodule on the anterior medullary velum. It is well known that this is certainly not so. On the contrary, the lobus anterius has progressively asserted itself. The beginning of this assertion is well seen in the lemurs (ELLIOT SMITH, 1903, *a* ; LE GROS CLARK, 1931) where the lobus anterius is not only quite large, but is actively pushing the fissura prima posteriorly against the pressure of the growing lobus medius, so that the main expansion of this is laterally and not anteriorly ; and the growth of the lobus anterius continues so that in Man it occupies about one-third of the dorsal surface of the cerebellum, and the fissura prima is readily seen as the fissure præclivalis.

It is the small size of the lobus medius, not the hypertrophy of the lobus anterius which links the Monotremes with the sub-mammalia. Outside the Primates, the only mammals whose cerebellum is at all comparable with that of the Monotremes are the peculiarly specialized Edentates. ELLIOT SMITH (1899, *a*) has shown that in these the lobus anterius is very large. This is especially marked in *Orycteropus* and

Choloepus, and the description by WOOLLARD (SONNTAG and WOOLLARD, 1925) confirms this for *Orycteropus*. The lobus medius in these animals is, however, better developed than in the Monotremes.

It is known that the expansion of the mammalian cerebellum depends upon the increase in cortical connections. In higher mammals this is expressed chiefly in the growth of the lobus medius; but since the lobus anterius also enlarges considerably, this must be due to similar causes. The Monotremes have practically no more lobus medius than the sub-mammalia, but they have large cerebral peduncles, a large pons, and a very large lobus anterius. The size of the lobus anterius must be due, therefore, to the number of cortical connections, but what is the cause of this one-sided development?

In marsupials and other primitive mammals with a small lobus anterius the pons is well developed but lies entirely anterior to the entering trigeminal nerve. There is, in fact, a wide gap between the pons and corpus trapezoideum through which the fifth nerve enters, and in which the commencement of the lateral lemniscus is plainly visible (STOKES, 1911). The trapezoid body is quite unencumbered by the pons, and the sixth, seventh, and eighth nerves are attached to its superficial surface. This condition is also found in the majority of other primitive mammals. One of the characteristic features of the Primate brain is the caudal extension of the pons to include the entering trigeminal nerve within its fibres. In the highest Primates the pons even covers the corpus trapezoideum so that the six, seventh, and eighth nerves are attached immediately against its caudal border, and their fibres pursue a horizontal course dorsal to its posterior extension. This fact appears to have been pointed out for the first time by HELD (1893), who regarded it as characteristic for the chimpanzee and Man. The Edentates, whose life so closely resembles that of *Echidna*, have also a marked retro-trigeminal pontine development.

In the Monotremes the only pons present lies wholly behind the fifth nerve, and in *Echidna* it covers the anterior part of the corpus trapezoideum, so that the sixth, seventh, and eighth nerves are attached immediately against its posterior border, fig. 3. There can be no doubt, then, that the pons in the Monotremes is the equivalent of that retro-trigeminal pontine development characteristic of the highest Primates, and that it is causally related to the great size of the lobus anterius of the cerebellum. The rostrum represents the aborted rudiment of the pre-trigeminal pons of all other mammals, and its failure of development is reflected in the primitive condition of the lobus medius.

Pathological evidence supports the view that the retro-trigeminal pons is related to the lobus anterius of the cerebellum. BIEMOND (1931) found that a localized lesion in the caudal part of the pons in Man was followed by degeneration in the lobus anterius—and especially in the culmen—of the cerebellum. Thus comparative and pathological evidence are in complete accord.

It has been shown that the one-sided development of the pons is reflected in the equally one-sided development of the cerebellum, but this provides no explanation for the eccentricity. The ultimate appeal must be to the other elements of the cortico-pontine system—the cerebral peduncles and hemispheres. This will be considered when the peduncles have been described.

In *Echidna* the paraflocculus forms the greatest part of the cerebellar hemisphere. This is due partly to the small size of the rest of the lobus medius, but essentially to the inherent development of the paraflocculus. According to HINES the paraflocculus in *Ornithorhynchus* is very small, but she failed to identify the fissura prima, and had considerable difficulty in tracing her pyramid to her paraflocculus. Finally, she has labelled as paraflocculus what appears to be part of the flocculus. It is quite clear from her figures, and particularly from a figure by ELLIOT SMITH (1895, fig. 3), that the paraflocculus in *Ornithorhynchus* is larger than that in *Echidna*.

The only mammals possessing a paraflocculus comparable to that in the Monotremes are the extinct Zeuglodonts. DART (1923) has shown that in these the paraflocculus is even larger than in *Ornithorhynchus*, so that it rises dorsally above the cerebral hemispheres. The other feature common to Zeuglodonts and Monotremes is the outstanding development of the trigeminal apparatus. In the endocranial casts of the Zeuglodonts the trigeminal nerve and Gasserian ganglion form a mass which almost equals in size the rest of the brain. DART naturally correlates the great size of the paraflocculi in the Zeuglodonts with the enormous hypertrophy of the trigeminal apparatus. The same explanation must hold for *Ornithorhynchus* and *Echidna*.

According to this author the fifth neuromere has played an important part in the development of the cerebellum. HERRICK (1924) has shown that trigeminal elements contribute largely to the formation of the auricle (the precursor of the flocculus and paraflocculus) in sub-mammalia. HORNE CRAIGIE (1928) describes a trigemino-cerebellar tract in the humming bird. HINES has stressed the importance of trigeminal contributions to the cerebellum in *Ornithorhynchus*, and in this account it has been shown that the trigeminal nerve sends fibres to the cerebellum in *Echidna* by every conceivable pathway. There are many accounts of trigemino-cerebellar connections in other mammals and there is every reason to believe that the trigeminal nerve contributes generously to the cerbellum throughout the vertebrate series, and that this contribution is particularly related to the paraflocculus.

In the Monotremes and Zeuglodonts the great size of the paraflocculi is an expression of the hypertrophy of the trigeminal apparatus. In most higher mammals the paraflocculi lack this excessive trigeminal support and are relatively much smaller. In addition, the enormous expansion of the rest of the lobus medius pushes them ventrally and laterally so that they become relegated to the base of the brain where they appear to have very little relation to their more progressive neighbour. At the same time the copula pyramidis becomes so stretched that it is barely recognizable as a thin connecting strip. In Man the paraflocculi are represented by the tiny " flocculi secundarii " of HENLE.

The cerebellum in the Monotremes is thus seen to be a strange mixture of primitive features and striking specializations. The most primitive feature is the deficient development of the non-parafloccular lobus medius. This is the only point of resemblance to the sub-mammalian cerebellum, and is a reflection of the aborted condition of the pre-trigeminal pons. The high degree of specialization is exhibited in the relatively enormous lobus anterius and paraflocculi. The size of the paraflocculi expresses the general trigeminal hypertrophy, that of the lobus anterius, a peculiarity of cortical connections which has evoked an almost purely retro-trigeminal development of the pons. In the pons and in the lobus anterius of the cerebellum, as in the posterior funiculi of the cord and their nuclei, the Monotremes have anticipated some of the most characteristic features of the brain of the highest Primates.

THE MID-BRAIN

The mid-brain in *Echidna* is distinctly mammalian in the possession of discrete inferior colliculi and of cerebral peduncles. The tectum is divided into the corpora quadrigemina of which the anterior, despite the poor visual development, are quite large, fig. 1. The inferior colliculi are well marked and are displaced rather ventrally and laterally. The lateral lemniscus can be seen passing to the inferior colliculi from which the inferior brachia pass to the diencephalon in the usual fashion. Even from the surface it is obvious that part of the lateral lemniscus reaches the brachium without interruption in the inferior colliculus. The superior brachia form thread-like continuations from the optic tracts to the tectum. They are easily detached from the surface of the brain. On the base of the mid-brain the large cerebral peduncles proceed caudally fig. 3. Between them lies the large ganglion interpedunculare, whose posterior pole is overlapped by the rostrum of the pons. The oculomotor nerves emerge from the medial sides of the peduncles just anterior to the ganglion interpedunculare. They are surprisingly big and almost equal the optic nerves themselves. The trochlear nerves are small and emerge from the anterior medullary velum in the customary manner. They were not attached to the brain figured.

The Auditory System—In the mid-brain the lateral lemniscus reaches the lateral periphery as soon as the fifth nerve has disappeared from the sections, fig. 14. On its medial side lies the ventral nucleus of the lateral lemniscus, which is simply a continuation of the medial part of the superior olive. HELD describes a similar condition for the cat, but in the opossum, according to STOKES, there is a distinct gap between the superior olive and the ventral nucleus of the lateral lemniscus. The great separation of corpus trapezoideum and pons in marsupials may explain this circumstance.

KÖLLIKER and ZIEHEN both commented upon the great size of the lateral lemniscus, but not all the fibres which ascend on the lateral border of the mid-brain belong to the lemniscus. The most peripheral fibres are passing from the trigeminal nerve to the tectum, and especially to the superior colliculus. Medial to these are tectopontine fibres and the ventral spino-cerebellar tract, which will reach the cerebellum along the brachium conjunctivum.

After the ventral nucleus has disappeared the dorsal nucleus of the lateral lemniscus is seen. This is not shown in the figures. It is large and lies medial to and among the fibres of the lateral lemniscus ventral to the inferior colliculus.

The nucleus of the inferior colliculus is lenticular and encapsuled by the fibres of the lateral lemniscus. Some of these end here, others cross the mid-line in the commissure, and about one-third pass on without interruption to the medial geniculate body, fig. 16. The inferior colliculus also receives trigeminal fibres. It emits fibres to the inferior brachium, some to the cerebellum and others to the opposite side by the commissure.

The inferior brachium contains two sets of fibres : superficial and deep. The superficial are fine, and lightly stained, and appear to be derived almost entirely from the inferior colliculus, fig. 14. The deeper fibres are much thicker and are the uninterrupted fibres from the lateral lemniscus. The superficial fibres end in the ventral nucleus of the medial geniculate body. A few deep fibres reach the

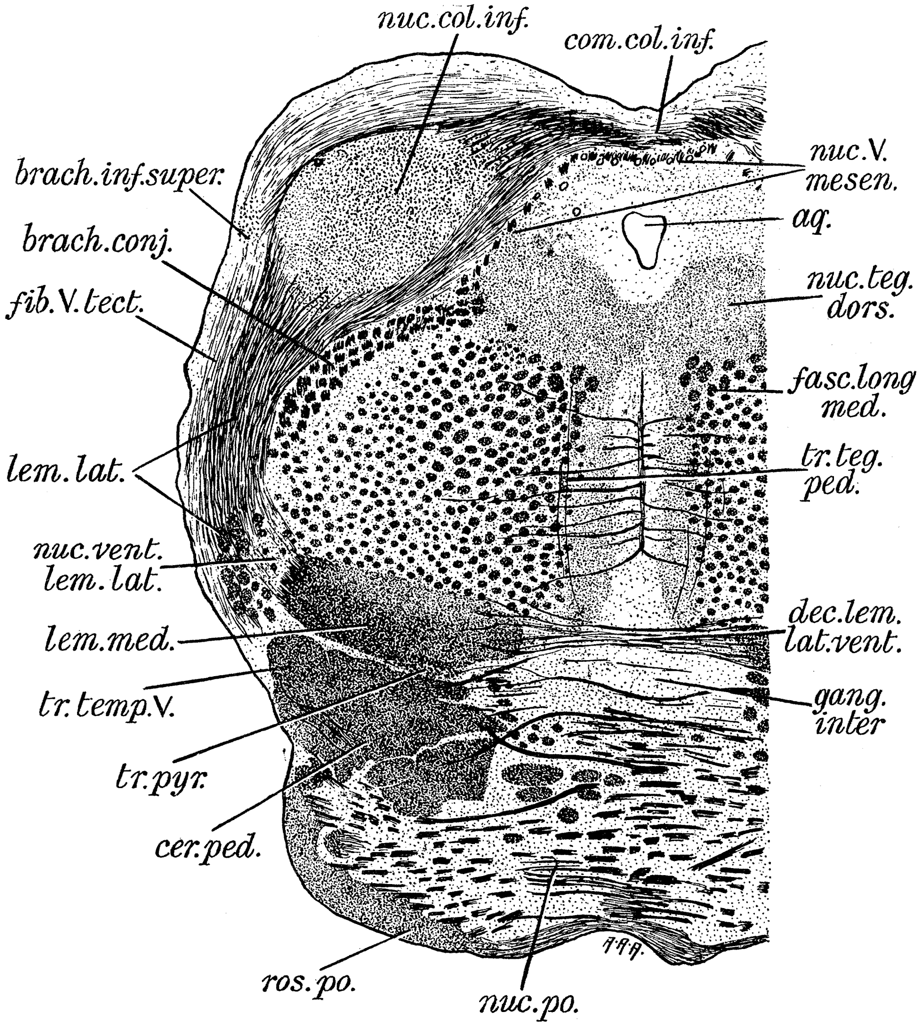

FIG. 14—Section through the inferior colliculus. × 10. The rostum is not sufficiently wide to include all the peduncular fibres and the tractus temporo-trigeminalis still lies outside. The superficial part of the inferior brachium is forming of fine fibres from the nucleus of the inferior colliculus. The pyramids lie immediately ventral to the medial lemnisci.

ventral nucleus, but the majority pass to the dorsal nucleus. Some fibres appear to pass from the lateral lemniscus to the superior colliculus. KÖLLIKER and ZIEHEN both described fibres passing from the medial lemniscus to the lateral, but most of these appear to reach the superior colliculus.

A lateral lemniscus is no mammalian peculiarity. It is well developed in fishes, and cannot, in them, be considered an auditory pathway. Indeed, in some deep-sea fishes where even a lagena is barely differentiated, the tract is enormous. The sub-mammalia possess, also, an intrinsic nucleus of the lateral lemniscus in the nucleus isthmi. The majority of authors—JOUSTRA (1918), KAPPERS (1921), LARSELL (1924), HUBER and CROSBY (1926), and others—consider the nucleus isthmi the homologue of the mammalian medial geniculate body. But PŘECECHTĚL (1925) pointed out that the nucleus isthmi shows a very close topographical similarity to the dorsal nucleus of the lateral lemniscus, and considered that the large-celled part of the nucleus isthmi became the dorsal nucleus of the lateral lemniscus while the small-celled portion might be represented in the medial geniculate body. More recently LE GROS CLARK (1933) has demonstrated that the medial geniculate body is a purely diencephalic derivative, and he regards the whole nucleus isthmi as represented in the dorsal nucleus of the lateral lemniscus.

The inferior colliculus of mammals is represented in lower animals by the torus semicircularis of reptiles, the nucleus mesencephali lateralis of birds, and the nucleus tegmentalis of lower fishes. Thus, long before the cochlea has attained the mammalian degree of perfection, and even when it is a barely recognizable rudiment, the cerebral stage is set for the reception of true auditory impulses, and the characteristic mid-brain paths are well, and sometimes conspicuously, developed.

Since such a complicated apparatus can exist in the absence of any peripheral mechanism for the reception of auditory inpulses, it is certain that its original function was not auditory but vestibular. Thus the auditory connections in the mid-brain, like those in the medulla oblongata, have evolved from the primitive vestibular connections. Whether auditory impulses in birds and reptiles ever reach the diencephalon to receive cortical recognition is doubtful. LARSELL (1924) has described a tractus isthmio-thalamicus in the frog, but the pars dorsalis diencephali in amphibia is so poorly differentiated that such impulses can scarcely be relayed to the cerebral hemispheres. It may be concluded that cortical representation in sub-mammalia, if it exists, is of minimum importance, and that the mid-brain centres—and especially the inferior colliculus or its representative—are quite competent to deal with any auditory impressions according to the requirements of these animals.

In *Echidna*, in addition to all the primitive vestibular apparatus, there is a definite increase in the importance of the auditory connections. Further, some of these pass through the mid-brain without interruption in the inferior colliculus to reach the dorsal nucleus of the medial geniculate body. This is a purely mammalian characteristic. It must be assumed that this new development has been occasioned by the enlargement of the cochlea ; that is, that it is probably an entirely auditory connection.

Since it is very doubtful if eighth nerve impulses reach the hemispheres in submammals, and equally doubtful whether the mechanism exists to deal with them effectively if they do, it is fairly certain that in this direct connection between the lateral lemniscus and the dorsal nucleus of the medial geniculate body in *Echidna* we have one of the first examples of an attempt to secure cortical recognition of hearing. It appears that in mammals probably the greater part of the incoming auditory impulses pass directly from the corpus trapezoideum—possibly even from the cochlear nuclei—to the dorsal nucleus of the medial geniculate body without interruption in the mid-brain and so reach the cerebral hemispheres.

The Medial Lemniscus—This is almost doubled in size after it receives its trigeminal component. In the caudal part of the mid-brain, fig. 15, the medial lemniscus

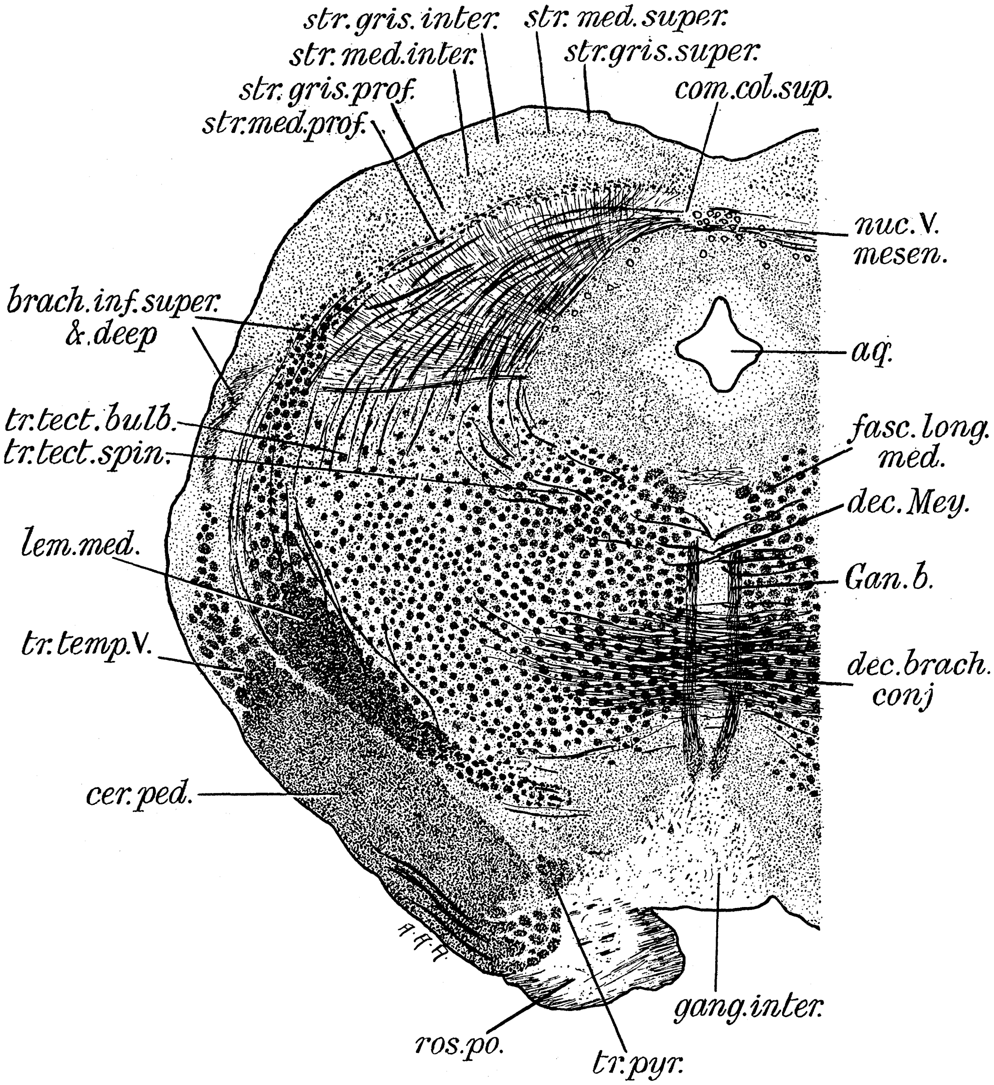

FIG. 15—Through the superior colliculus. × 10. The superficial and deep strata of the inferior brachium are clearly shown. The mesencephalic nucleus of the fifth nerve displays its typical distribution. The pyramids are beginning to leave the medial border of the cerebral peduncle.

lies immediately dorsal to the cerebral peduncles, and there may be some interchange of fibres as Kölliker and Ziehen suppose. More anteriorly the lemniscus passes dorsally and the substantia nigra partly occupies the interval so formed, fig. 16. The medial lemniscus contributes many fibres to the superior colliculus, fig. 15; these end chiefly in the stratum griseum intermedium. The lemniscus ends in the ventral nucleus of the thalamus which encroaches upon the anterior part of the mid-brain.

In the posterior part of the mesencephalon are the dorsal and ventral commissures of the lateral lemniscus, fig. 14, described by Winkler and Potter. The dorsal commissure—the commissure of Probst—appears to connect the lateral lemniscus with the medial longitudinal fasciculi as described for the opossum by Stokes. The ventral commissure—in *Echidna* at least—appears to have little to do with the lateral lemniscus; its connections are chiefly with the medial lemnisci.

The Brachia Conjunctiva—These arise from the lateral cerebellar nucleus, fig. 14. As they pass forwards and ventrally they are joined by trigeminal and ventral spino-cerebellar fibres running in the reverse direction to the cerebellum. More anteriorly the brachia lie between the mesencephalic root of the fifth nerve and the lateral lemniscus, and soon cross in the mid-line to end in the pars magnocellularis of the red nucleus.

The Red Nucleus—The red nucleus comprises large and small-celled elements. The large-celled lies posteriorly and medially. It receives the brachium conjunctivum, fig. 15, and gives rise to the rubro-spinal tract. The small-celled part lies laterally and more anteriorly and its limits could not be defined with certainty. Fibres which arise from the red nucleus and pass forwards into the sub-thalamus probably constitute the field B.A.T.H., or *H* of Forel.

The Cerebral Peduncles—In the anterior part of the mesencephalon the peduncles are separated by a wide interval from the medial lemnisci. At this level they comprise from lateral to medial border tractus temporo-trigeminalis, cortico-pontine and arcuate fibres and pyramidal tract. More posteriorly the peduncles lie immediately ventral to the medial lemnisci and soon commence to enter the rostrum of the pons.

Substantia Nigra—This is composed of large cells which appear to be pigmented in these sections, fig. 17. The cells are restricted to the medial border of the peduncles in close relation to the pyramidal tract and the ventral tegmental nucleus. This is in sharp contrast to the condition in the opossum, as described by Tsai (1925, *b*), where the substantia nigra lies at the lateral border of the peduncle, separated by a wide interval from the ventral tegmental nucleus.

The Ventral Tegmental Nucleus—The nuclei of both sides meet in the mid-line to form a continuous cell mass. The cells are large and extend laterally, dorsal to the substantia nigra, fig. 17. According to Kosaka and Hiraiwa (1915) the ventral tegmental nucleus is merely an extension of the substantia nigra. Certainly, in *Echidna*, the cell masses are in continuity, but the cells of the ventral tegmental nucleus are smaller and lack any characteristic pigmentation. Further, Tsai has shown that in the opossum, where the ventral tegmental nucleus is well developed, the substantia nigra lies completely separate at the lateral border of the peduncle. The nucleus receives fibres from the corpus mamillare by the tractus mamillo-tegmentalis. No other connections could be traced.

The Ganglion Interpedunculare—This forms a very large mass on the ventral surface of the mid-brain between the cerebral peduncles. Posteriorly it is covered by the rostrum of the pons, anteriorly it almost reaches the corpus mamillare, fig. 3. The ganglion is composed of small, closely packed cells in which no nuclear distinction was obvious. Throughout its length tegmento-peduncular fibres enter the dorsal surface. They arise from the dorsal tegmental nuclei and pass antero-ventrally to reach the ganglion. The anterior one-third of these fibres are gathered into the compact bundle of GANSER. The fasciculi retroflexi enter the anterior pole of the ganglion and decussate before passing among the cells, fig. 16.

The Dorsal Tegmental Nuclei—These lie in the central grey matter of the mid-brain and meet in the mid-line ventral to the aqueduct. They are large and composed of closely packed cells, fig. 14. There are two chief sets of fibre connections. The dorsal pass from the lateral angle of each nucleus to the lateral lemniscus of the same side and its dorsal nucleus. This may be called the *tractus tegmento-lemniscalis*. The ventral connections are more conspicuous. KÖLLIKER described *fibræ longitudinales dorso-ventrales* arising from the medial longitudinal fasciculus and passing ventrally to the pons and to the ganglion interpedunculare. ZIEHEN questioned their origin from the medial longitudinal fasciculus, but thought that some of the fibres might reach the pons; these he called the *fibræ rectæ pontis*. He correctly described the origin of the remainder from the dorsal tegmental nucleus and their termination in the interpeduncular ganglion. These can be described as the *tractus tegmento-peduncularis*. ZIEHEN also described GANSER's bundle correctly; it is really a more compact massing of the anterior tegmento-peduncular fibres, fig. 15.

The Trochlear Nerve—The fourth nucleus is composed of scattered small motor cells lying among and dorsal to the medial longitudinal fasciculus. The root-fibres pass across the ventral part of the central grey matter to reach the medial border of the mesencephalic root of the fifth nerve. They hug this closely as they run dorsally and medially to the anterior medullary velum, there to decussate and emerge, fig. 13.

The Oculomotor Nerve—Unlike the condition in the opossum, there is, as KÖLLIKER and ZIEHEN noted, a wide interval between the fourth and third nuclei. This gap is partly occupied by scattered cells similar to those of the two chief nuclei. The third nucleus is very large and reaches almost to the diencephalon. Its cells are like those of the fourth nucleus and lie just dorsal to the medial longitudinal fasciculi, fig. 16. Between the two nuclei is a mass of very small cells which may represent the EDINGER-WESTPHAL component. The fibres of the nerve collect ventral to the nucleus and pass forwards and ventrally, accumulating as they go. At the anterior level of the nucleus they lie just dorsal to the anterior pole of the ganglion interpedunculare, fig. 17. Here they pass laterally, posterior to or through the fasciculus retroflexus, and emerge from the medial border of the cerebral peduncle anterior to the interpeduncular ganglion.

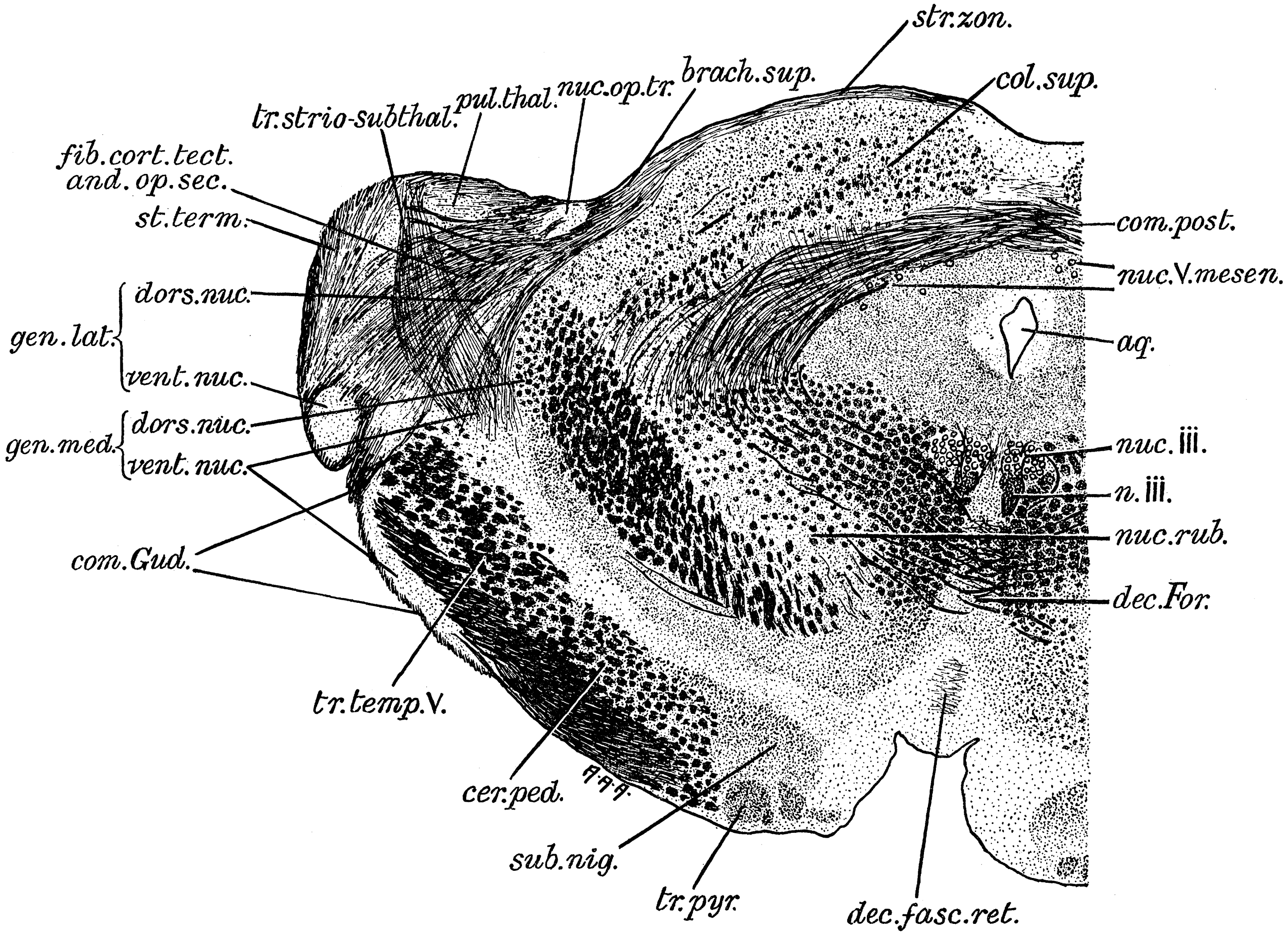

FIG. 16—Through the superior colliculus and the pulvinar. × 10. The deeper part of the inferior brachium is entering the ventral nucleus of the thalamus. The ventral nuclei of the geniculate bodies are continuous medially with the sub-thalamus. The origin of the commissure of Gudden is shown. The pyramids and the substantia nigra are confined to the medial border of the peduncles.

The Superior Colliculus—The superior colliculi are well developed and their functions are clearly not chiefly visual. It is possible to distinguish seven layers: Stratum zonale (which TSAI, 1925, *a*, does not consider a separate layer), Strata griseum and medullare superficiales, strata griseum and medullare intermedia, strata griseum and medullare profunda, fig. 15. TSAI states that optic fibres do not pass in the stratum zonale; in *Echidna* they appear to do this before reaching the stratum opticum, fig. 16.

In addition to visual fibres—which form a very poor contribution—the superior colliculus receives fibres from the fifth nerve, the medial lemniscus, the lateral lemniscus, and the cerebral cortex. Most of the afferent fibres appear to end in the stratum griseum intermedium. The efferent fibres arise chiefly from the stratum griseum profundum and are widely distributed. The most obvious form the fountain radiations of MEYNERT, fig. 15. These give rise to two tracts, the tecto-bulbar and tecto-spinal. The tecto-bulbar fibres collect in the lateral part of the tegmentum medial to the brachium conjunctivum and lateral lemniscus. They appear to be mostly uncrossed. The tecto-spinal tracts pass more directly ventrally, close to the central grey matter. They cross in the mid-line in the dorsal tegmental decussation of MEYNERT to form the tecto-spinal tract of the opposite side. Many fibres radiate from the stratum griseum profundum into the central grey matter. Other connections are with most of the thalamic nuclei (tractus tecto-thalamicus), with the nucleus reuniens (tractus tecto-reuniens), with the hypothalamus (tractus tecto-hypothalamicus), with the nucleus pretectalis (tractus tecto-pretectalis), with the pons (tractus tecto-pontinus) and with the cerebellum (tractus tecto-cerebellaris).

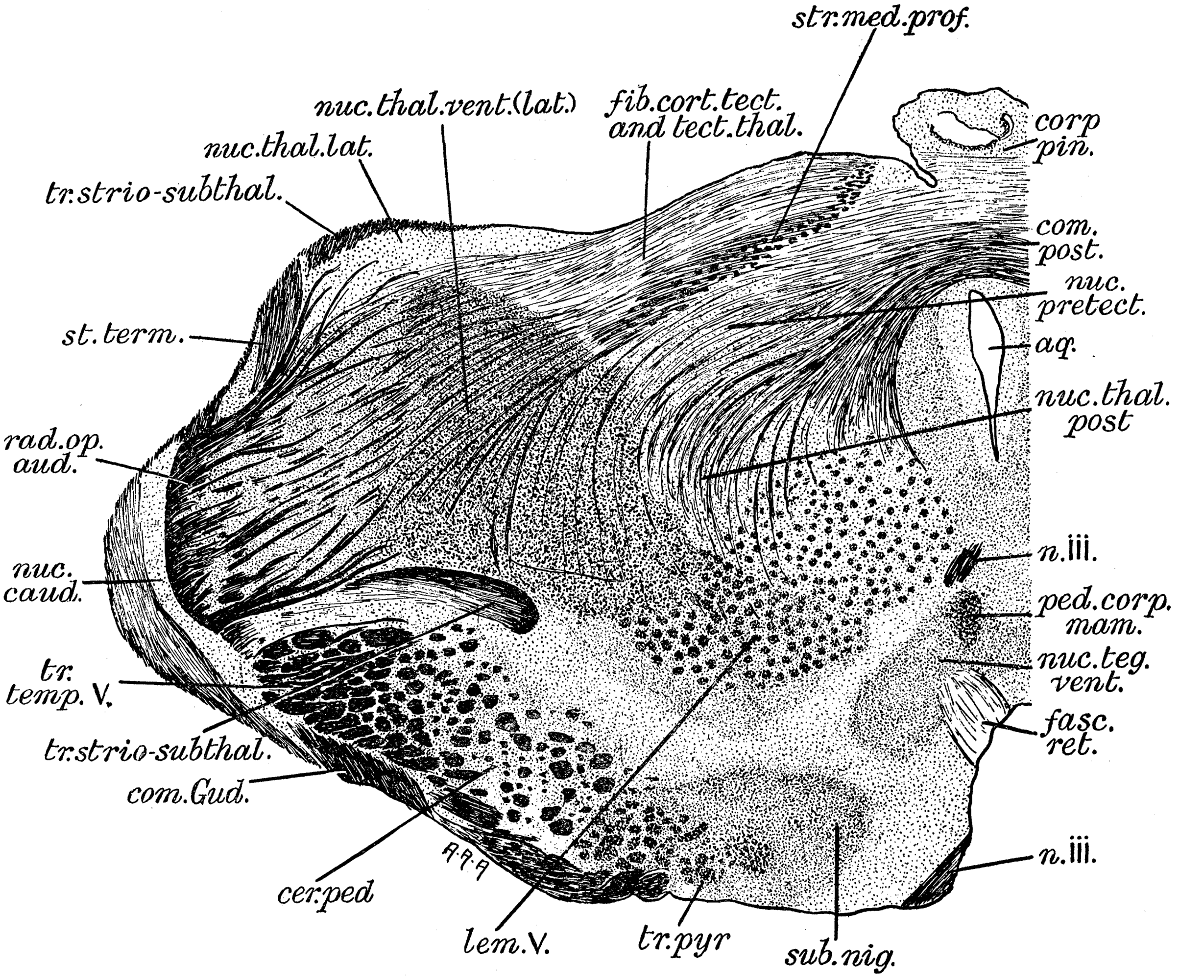

FIG. 17—Through the pineal body. × 9. The lateral part of the medial lemniscus is entering the pars lateralis of the ventral nucleus of the thalamus. The great development of the pars intercalaris encephali is indicated in the diffuse extent of the nuclei pretectalis and posterior thalami.

The fibres to the pons pass caudally along the lateral lemniscus, those to the cerebellum join similar fibres from the inferior colliculus, and both pass through the anterior medullary velum.

The Ventral Tegmental Decussation—According to ZIEHEN there is no decussation of FOREL in *Echidna*. In fig. 16 it can be seen to arise in the usual manner from the pars magno-cellularis of the red nucleus. After decussation the fibres run caudally in the tegmentum until they reach the pons. There they come into relation with the ventral spino-cerebellar tract and the two run together as the " aberrirendes Seitenstrangsbündel " of VON MONAKOW. In the medulla oblongata this bundle lies just medial to the nucleus arcuatus trigemini, fig. 8.

The Medial Longitudinal Fasciculus—This tract is well developed. Anteriorly it is lost in the pars ventralis diencephali, posteriorly it extends throughout the brain-stem to the anterior funiculi of the cord. In the mid-brain it is in close association with the third and fourth nuclei ; in the medulla oblongata it receives many additions from the vestibular nuclei by the dorsal internal arcuate fibres, the decussation of VON MONAKOW, the decussation of the nucleus of BECHTEREW, and the commissure of PROBST. Probably some cochlear fibres also join this tract. As described above, dorsal secondary reflex fibres from the trigeminal nerve are closely related to this tract in the medulla oblongata and mid-brain. They appear to form a similar reflex path linking the fifth nerve with the oculomotor nuclei.

An indefinite nucleus of the medial longitudinal fasciculus was identified as the nucleus of DARKSCHEWITCH. This receives fibres from the posterior commissure as well. I cannot confirm the statement of ZIEHEN that the nucleus of DARKSCHEWITCH is conspicuous.

Between mesencephalon and diencephalon lies an indeterminate region whose structures cannot be assigned with certainty to either. Most of these structures are usually described with the diencephalon, but in this paper they are considered separately, because they appear to represent a higher mesencephalic level rather than a portion of the diencephalon proper.

The Nucleus Pretectalis—This is large and diffuse, fig. 17. It receives fibres from the medial lemniscus, the posterior commissure and the superior colliculus, but optic tract collaterals—if they exist as in other mammals—are not obvious. The nucleus lies in the lateral tegmentum and extends anteriorly, medial to the fasciculus retroflexus. It gives off a large tractus pretectalis descendens which could not be followed beyond the tegmentum. Numerous fibres pass to the thalamus, some to the habenular ganglion, some to the pars ventralis diencephali, and possibly some to the cerebral cortex. It corresponds to the nucleus which ZIEHEN identified as nucleus " X."

According to LE GROS CLARK (1932, *b*) the precursor of the pretectal nucleus is the *pars intercalaris diencephali* (of HERRICK) of amphibia. In reptiles this becomes, highly differentiated into a series of discrete nuclei—pretectalis, geniculato-pretectalis, spiriformis. In birds there is even greater complexity. In mammals there is less differentiation and the whole group is represented by the nucleus pretectalis.

Huber and Crosby (1926) have described various nuclei of the posterior commissure in the reptile and, considering the close relation which the mammalian nucleus pretectalis bears to the posterior commissure, it is probable that these nuclei may also be included in the diffuse nucleus pretectalis.

The Posterior Nucleus of The Thalamus—This is a diffuse mass of cells lying ventral and lateral to the nucleus pretectalis, fig. 17. The two cells masses are poorly differentiated. The fibre connections of this nucleus are not clear. It appears to receive some fibres from the medial lemniscus and to transmit others to the hypothalamus. It may correspond to the nucleus which Ziehen described as an extraordinarily large nucleus of Darkschewitch. The indefinite posterior thalamic nucleus described by Hines for *Ornithorhynchus*, and the posterior thalamic nucleus of Gurdjian (1927) appear to be similar structures. The relations of this nuclear mass seem to be much more mesencephalic than diencephalic, and it appears probable that this, together with the nucleus pretectalis, represents the combined nuclei pretectalis, geniculato-pretectalis, spiriformis and nuclei of the posterior commissure described by Huber and Crosby for the alligator ; the pars intercalaris diencephali of amphibia.

The Large-Celled Nucleus of the Optic Tract—This is a small but well-circumscribed group of cells lying within the optic fibres of the superior brachium, fig. 16. Some optic fibres certainly end here, but it is by no means " large-celled." The small size, and the absence of large cells, probably reflect the poor visual development in *Echidna*. Rioch (1931) and Le Gros Clark (1932, *b*) regard this nucleus as the mammalian representative of the reptilian nucleus lenticularis mesencephali. In mammals, according to Le Gros Clark, it is gradually buried by the great expansion of the higher physiological levels of the pars dorsalis diencephali which produces the caudal projection of the pulvinar thalami. In *Echidna* the caudal projection of the thalamus is occasioned by the expansion of the lower physiological level—the ventral nucleus. This extends lateral, not dorsal, to the tectum and the large-celled nucleus of the optic tract lies free on the surface.

The Posterior Commissure—This is very conspicuous in *Echidna* and can be divided into upper and lower portions. The upper lies more frontally in the posterior part of the pineal stalk, the lower is continuous posteriorly with the commissure of the superior colliculus. The dorsal fibres pass widely laterally and come into close relation with the nucleus pretectalis where many end, the remainder run ventrally, close to the central grey matter, into the tegmentum, fig. 16. These also contribute fibres to the nucleus pretectalis, the rest end close to the medial longitudinal fasciculus. Some fibres certainly join the fasciculus, others seem to end in its nucleus.

There does not appear to be any discrete nucleus of the posterior commissure. The nucleus so described by Rioch (1931) for carnivora appears to be the nucleus pretectalis which is closely associated with the posterior commissure.

The Fasciculus Retroflexus—The habenulo-peduncular tract is very large. It arises as medial and lateral divisions which pass ventrally, laterally, and posteriorly and

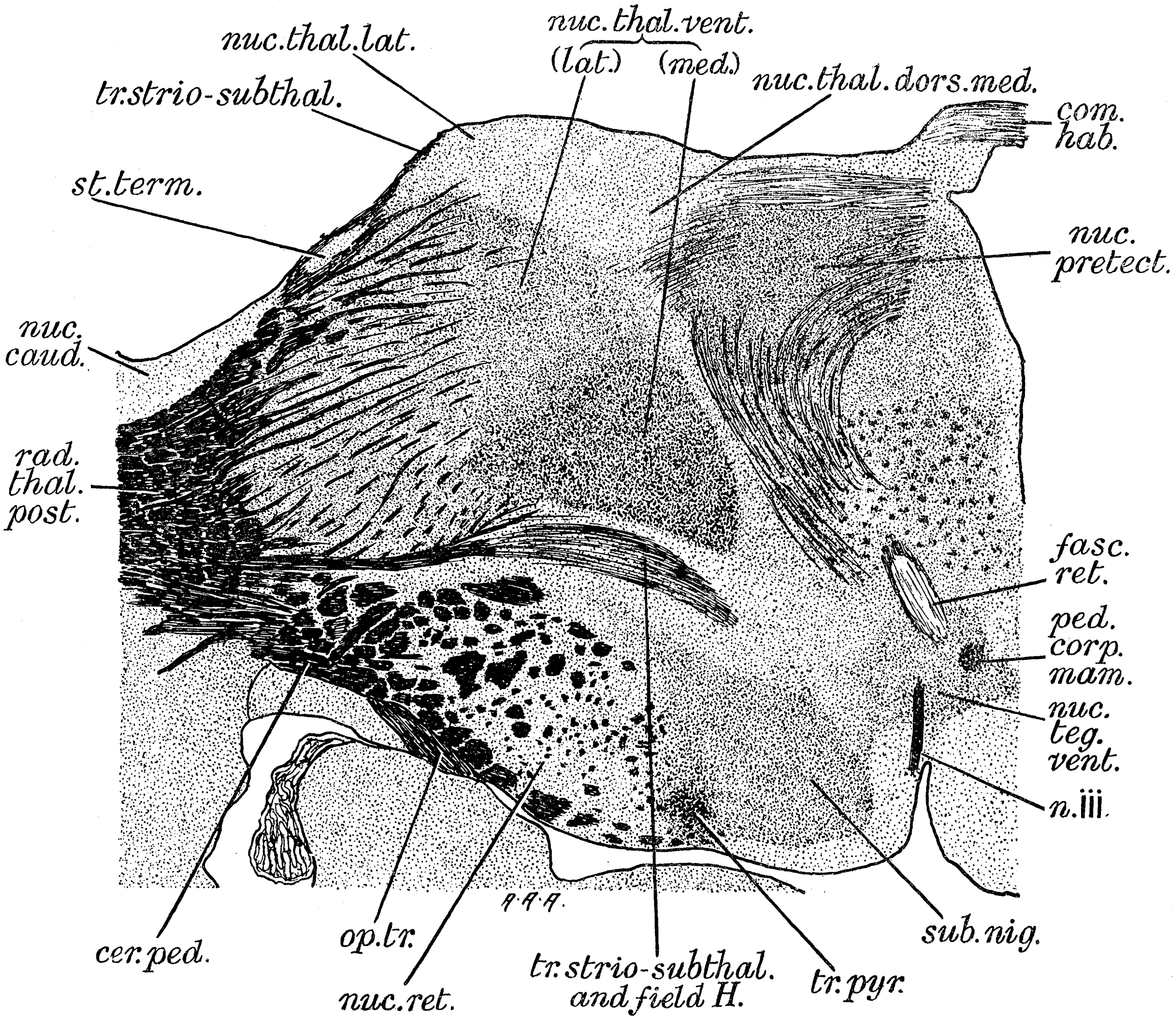

FIG. 18—Through the posterior thalamic radiation. × 10. The medial part of the medial lemniscus is entering the pars medialis of the ventral nucleus of the thalamus. The two parts of the ventral nucleus are well differentiated. The lateral nuclei of the thalamus are poorly differentiated from the ventral group.

join, fig. 19. The combined divisions run more posteriorly and ventrally, and then gradually medially so that they pass anterior to the emerging third nerve just dorsal to the interpeduncular ganglion, fig. 18. The fasciculi enter the anterior pole of the ganglion where they decussate before ending amongst the cells.

The fasciculus is composed of a thick core of lightly stained gelatinous-looking fibres enclosed in a thin capsule of fine, darkly stained fibres, fig. 18. The central core may represent the non-myelinated fibres of birds; if so, the non-myelinated fibres arise from both habenular nuclei and not solely from the medial as described by HUBER and CROSBY (1929, *b*) for the dove and by others for mammals.

In *Echidna* there are many ascending fibres in the fasciculus retroflexus. These

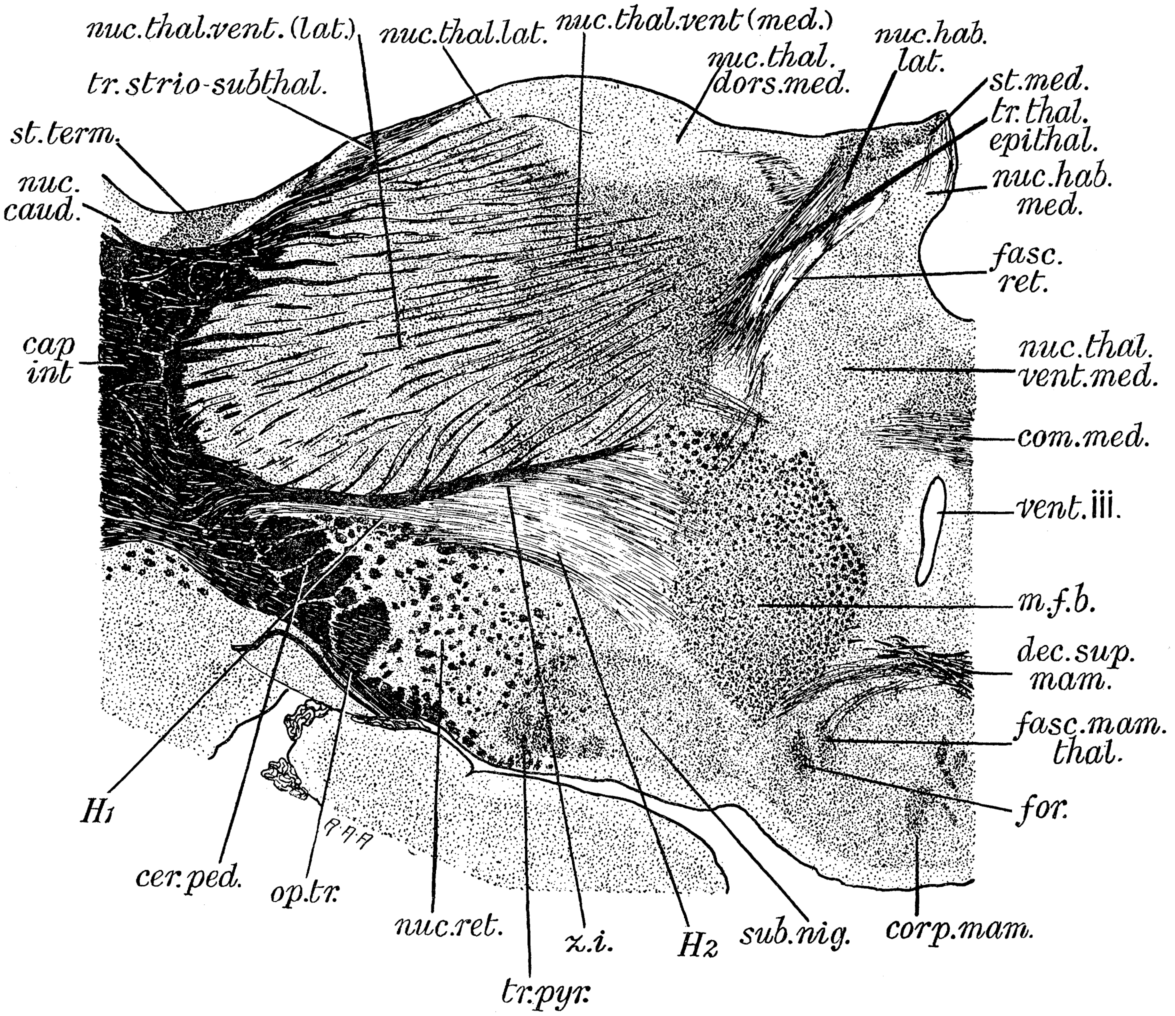

FIG. 19—This illustrates the poor differentiation of the lateral group of nuclei from the two parts of the ventral. The origin of the fasciculus retroflexus is shown ; it has a core of non-myelinated fibres. The large corpus mamillare and the supra-mamillary decussation can be seen. × 9.

arise chiefly from the pars medialis of the ventral nucleus of the thalamus, fig. 19. Some end in the habenular region, but the majority reach the stria medullaris without interruption. This band of fibres, which may be designated the *tractus thalamo-epithalamicus*, connects the trigeminal end-station in the thalamus with the olfactory apparatus, thus linking tactile sensibility of the head and mouth with smell. This is the well-known " oral sense " of EDINGER and KAPPERS, but I believe that this is the first occasion on which an anatomical basis for this oral sense has been demonstrated. WOOD JONES' observations support the functional existence of such a tract : he says (1923, p. 45) " In this testing it is not only the sensitive skin (of the snout) which is called into play, for judging by the frequent inspiratory sniffs which form the accompaniment of most of *Echidna's* activities, the sense of smell is an important guiding factor."

The Inferior Brachium—This has already been described as comprising a superficial tract of fine fibres which reach the ventral nucleus of the medial geniculate body and probably convey vestibular impulses, and a deeper stratum of thick fibres which end in the dorsal nucleus and certainly carry auditory impulses. Some of these deep fibres also reach the ventral nucleus. Since some fibres probably pass from the dorsal nucleus of the lateral lemniscus to the commissura transversa of Gudden (*tractus commissura transversa* of Larsell) these must also run in the inferior brachium.

The Superior Brachium—This is a thin thread of fibres running from the optic tract to the superior colliculus, fig. 2. It conveys the mesencephalic optic root of Tsai (1925, *a*) and is as poorly developed as the rest of the visual apparatus. Among the fibres lies the large-celled nucleus of the optic tract.

The whole of this intermediate region appears to represent an advance upon the general mesencephalic mechanism. In the Sauropsida with their poorly evolved fore-brain the intermediate region is highly differentiated, and this is more obvious in birds whose pallium is more rudimentary than in reptiles. In mammals, with the growth of the fore-brain, the region progressively diminishes in importance. In *Echidna* it is represented by the large nucleus pretectalis, the nucleus posterior thalami and possibly the large-celled nucleus of the optic tract, and the condition in *Ornithorhynchus* appears to be very similar. But in higher mammals the nucleus pretectalis is relatively very much smaller and the nucleus posterior thalami is scarcely distinguishable from the thalamic nuclei.

The nuclear masses in this region receive, like the tectum, impulses from all the sensory pathways. Similarly, they possess their own efferent tracts which do not supersede, but supplement, those of the tectum. They are closely connected with the mid-brain and lower centres on the one hand, and with the fore-brain on the other, and act as an intermediary between the two—an advance upon the tectum but inferior to the fore-brain. In the Sauropsida the development of this region appears to be an attempt to obtain a more efficient integration than is possible to the tectum. So it is really a *neo-tectum*. But with the advance of the neopallium it loses in importance and its retrogression proceeds hand in hand with the growth of the cerebral hemispheres which correlate all the mechanisms of lower centres and add that leaven of conscious appreciation and intelligent direction so characteristic of higher mammals.

The name " Pars Intercalaris Encephali " expresses well the topographical and physiological position of this region.

The Diencephalon

The diencephalon, as seen from the exterior, is very large, figs. 1 and 2. Its bulk is due chiefly to the enormous hypertrophy of the ventral nucleus of the thalamus which projects caudally in a large " pulvinar " reminiscent of that of Primates. That this " pulvinar " is homologous in part with that of Primates is a rather astonishing fact which depends, however, not upon the intrinsic size of the pulvinar, but upon the great expansion of the ventral nucleus. This is further emphasized by the relation of this " pulvinar " to the mid-brain. A true pulvinar—as seen in Primates—is an expression of the enlargement of the higher physiological levels of the thalamus, and it projects caudally dorsal to the tectum. But in *Echidna* the projection is lateral to the mid-brain and is due, not to the size of the higher physiological level, but to the hypertrophy of the lower.

At the caudal border of the " pulvinar," and in the course of the optic tract, is a fusiform swelling, the lateral geniculate body. This was present on both sides of the diencephalon in the six *Echidna* brains examined, and was described by ZIEHEN (1897, *a*). That it is not always present in *Echidna* is shown by the fact that it was absent from the brain-stem described by ELLIOT SMITH (1902). It is small, in keeping with the size of the optic tract, and is continued dorsally in the superior brachium. Medial to the lateral geniculate body, and rather more caudally, is a low swelling over the anterior end of the inferior brachium and the lateral border of the cerebral peduncle, fig. 1. This is the medial geniculate body. It was so described by ZIEHEN (1897, *a*) " subject to microscopic confirmation." A medial geniculate body was not externally obvious in the brain-stem described by ELLIOT SMITH and he rightly concluded that hearing is not an important function in *Echidna*. Of the six brains examined, only one possessed well-marked medial geniculate bodies. In the others the swelling was less conspicuous or even absent. The projection of this body is due, not to its inherent size, but to the projection of the lateral border of the underlying cerebral peduncle and is, therefore, liable to considerable variation. Although ZIEHEN (1908) finally concluded that the medial geniculate body in *Echidna* lay elsewhere, this swelling does represent part of the medial geniculate body as its relation to the inferior brachium illustrates. It shares with the outward manifestation of the lateral geniculate body the peculiarity that it represents the ventral nucleus only of the geniculate bodies of higher mammals.

The epithalamus is conspicuous. The habenular ganglia present obvious protuberances from both dorsal and medial aspects, figs. 2 and 4. The striæ medullares run anteriorly and ventrally around the dorso-medial border of the diencephalon. They appear deceptively small to superficial examination.

The corpus mamillare is very large and unpaired. It presents a hemispherical swelling which extends caudally almost to the anterior pole of the ganglion interpedunculare.

The hypophysis forms a large, thin-walled sac continuous by a wide opening with the third ventricle. It is incompletely bilobular. Posteriorly it projects slightly beyond the corpus mamillare. Its walls are attached laterally to the tuber cinereum and posteriorly to the mamillary body. There is no obvious distinction of nervous and buccal components. In the majority of brains examined the anterior wall of the hypophysis joined the infundibulum in the usual manner so that a definite post-optic recess was present. In the specimen shown, fig. 4, the optic chiasma lay in the anterior wall of the junction of hypophysis and infundibulum and the tracts passed in the lateral walls of the infundibulum. Thus the post-optic recess lies in the opening of the infundibulum, and the anterior wall of the hypophysis is continuous with the lamina terminalis.

The optic nerves are tiny, as is the chiasma. According to SCHUSTER (1910) the optic nerves in *E. setosa* are much larger than those in *E. aculeata*, so the Tasmanian species may possess better vision. The optic tracts run widely laterally and posteriorly round the base of the brain in close relation to the cerebral peduncles. They join the lateral geniculate bodies, fig. 3.

A large massa intermedia connects the two thalami, fig. 4.

In the subsequent description the diencephalon is regarded as being composed of a pars dorsalis, or thalamus proper, and a pars ventralis comprising the sub- and hypothalami. This conforms to the nomenclature of LE GROS CLARK (1932, *b*), and as far as the pars dorsalis diencephali is concerned, his classification of the nuclei, which is at once the simplest and most logical yet proposed, is followed as far as possible.

THE PARS VENTRALIS DIENCEPHALI

The Subthalamus

The absence of reliable cell material rendered the identification of the nuclei in the subthalamus and hypothalamus uncertain. In the subthalamus two nuclei only could be recognized ; the corpus subthalamicum of LUYS or lateral nucleus, and a medial subthalamic nucleus, fig. 20. These correspond with ZIEHEN's nuclei ϕ and ϕ' respectively. In *Ornithorhynchus* HINES has effected a further subdivision of the medial nucleus. The cells of the corpus subthalamicum are large and lightly stained and the nucleus is a marked feature in sections through this region. The cells of the medial nucleus are smaller and scattered. The corpus subthalamicum receives many fibres from the region of the red nucleus. These pass forwards in the field H of FOREL and appear to divide into the fibres of fields H_1 and H_2 in the usual fashion. Field H_1 passes anteriorly dorsal to the subthalamic body. Here some of its fibres end, others join the ansa lenticularis. Field H_2 lies more medially and ventrally. It contributes fibres to the subthalamic body and the remainder pass towards the hypothalamus where they are lost. The ansa lenticularis runs medially from the base of the internal capsule to the corpus subthalamicum. The zona incerta lies dorsal to field H_1, between it and the ventral nucleus of the thalamus.

It can be seen, fig. 16, that the posterior subthalamic region extends laterally to become continuous with the ventral nuclei of the medial and lateral geniculate bodies. The ventral nucleus of the lateral geniculate body is the better defined and forms the fusiform swelling in the optic tract. It receives optic fibres some of which end there, others pass on to the dorsal nucleus and tectum. The ventral nucleus gives rise to secondary fibres which pass dorsally and posteriorly over the periphery of the pulvinar to reach the superior colliculus. Some fibres from the ventral nucleus appear to join the commissure of GUDDEN.

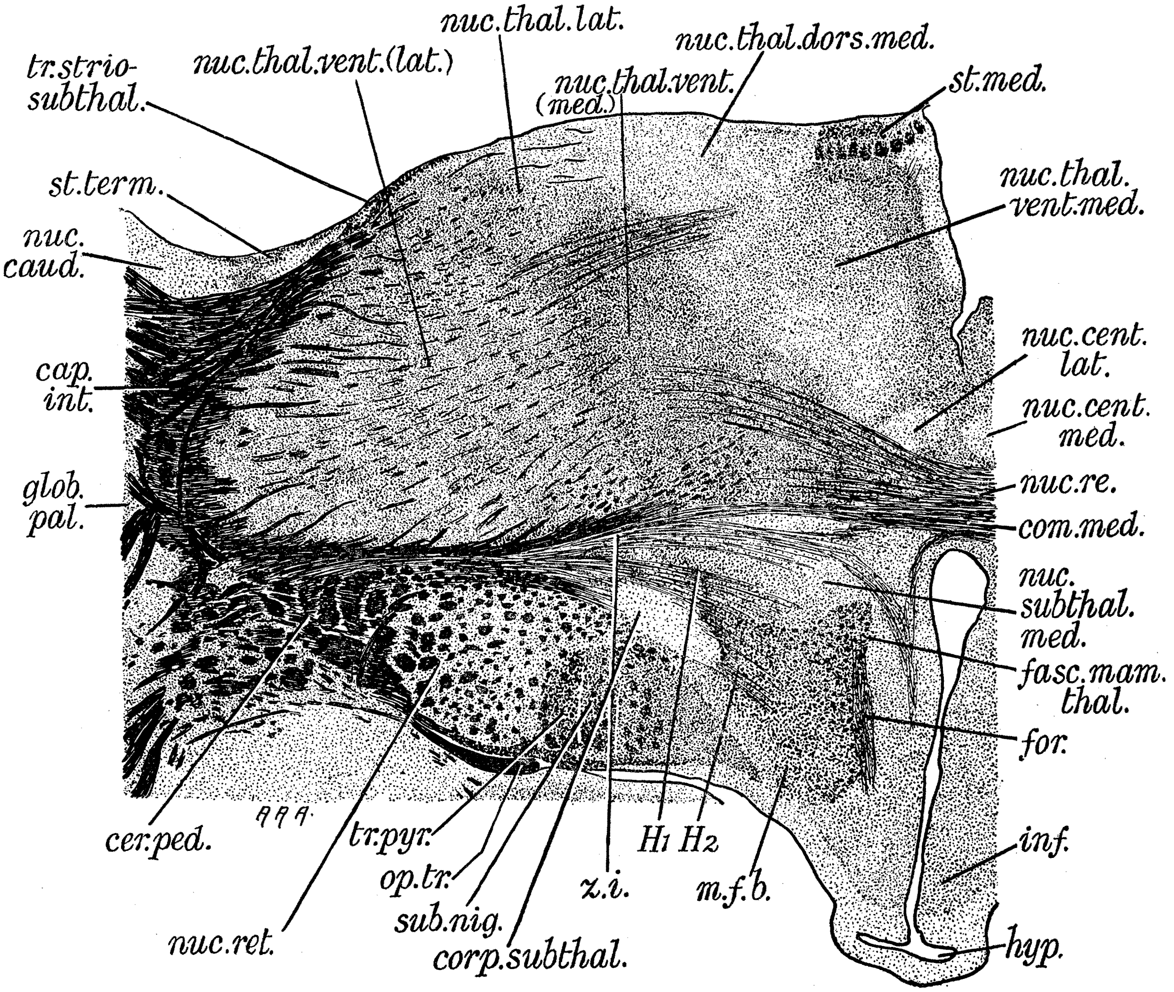

FIG. 20—This section passes through the widest part of the pars dorsalis diencephali and displays the chief nuclei in their typical relationship. The nucleus ventralis medialis is very large. The corpus subthalamicum is lightly stained. The small fornix and the fasciculus mamillo-thalamicus are difficult to distinguish at the medial border of the medial forebrain bundle. The substantia nigra and the pyramid can still be detected at the medial border of the peduncle. × 9.

The ventral nucleus of the medial geniculate body is a diffuse lateral and dorsal extension of the subthalamus. The dorsal part lies against that part of the ventral nucleus of the thalamus which receives direct auditory fibres (and represents the dorsal nucleus of the medial geniculate body) and receives the superficial fine fibres which have arisen from the inferior colliculus. The lateral extension passes externally as a thin layer over the lateral border of the cerebral peduncle, fig. 16. From the whole of its superficial extent fibres pass ventrally to join the commissure of GUDDEN.

The substantia nigra accompanies the cerebral peduncles in their passage through the subthalamic region, fig. 19. It is always related closely to the pyramidal tracts which lie at the medial border of the peduncles. The cells of the substantia nigra reach anteriorly to the base of the internal capsule. The fibres of the peduncles are rather scattered amongst a large collection of cells. In this mass ZIEHEN distinguished four nuclei. The substantia nigra appears to represent his two medial nuclei, the others may be grouped as the nucleus reticularis.

The pyramidal fibres are the first to leave the hemisphere to commence the formation of the cerebral peduncles. They arise from the most anterior area of the hemisphere—area 3 of SCHUSTER (1910). The other fibres in the peduncle all arise posterior to the pyramidal tract—from area 4 of SCHUSTER—and when they enter the peduncle they push the pyramids medially. The last fibres to join are those of the tractus temporo-trigeminalis which occupy the lateral border of the peduncles. Thus no peduncular fibres arise from any cortical area anterior to that which gives rise to the pyramidal tracts ; that is, there are no fronto-pontine fibres in the cerebral peduncles.

The *tractus strio-subthalamicus* of this paper corresponds to the " Kometenbündel " of ZIEHEN. It arises anteriorly in the medial part of the corpus striatum and runs caudally on the dorso-lateral periphery of the diencephalon close to the medial border of the stria terminalis, fig. 18. ZIEHEN stated that the anterior part of this tract passed ventral to the anterior commissure, but it appears to pass mostly or entirely dorsal to this. Among its fibres is a definite nucleus. The tract reaches the caudal border of the diencephalon where it bends ventrally in a wide arc before running anteriorly into the subthalamus. Most of its fibres are dissipated in the subthalamus and some reach the subthalamic body itself. The apex of the arc, fig. 16, incompletely separates the ventral nucleus of the lateral geniculate body from the rest of the subthalamus. Here many optic fibres pass through the tract and increase its apparent bulk considerably. The tractus strio-subthalamicus appears to be an especially differentiated part of the stria terminalis most of whose course it closely follows. Like the stria it has its own nuclear development.

The subthalamus in *Echidna* differs little from that of other mammals although the tractus strio-subthalamicus might be considered a peculiarity. The fact that the ventral nuclei of the medial and lateral geniculate bodies are extensions of the subthalamus is in accordance with their phylogenetic history. KAPPERS (1921) and LE GROS CLARK (1932, *a*) have shown that the ventral nucleus of the lateral geniculate body has evolved from the subthalamus, and the latter author (1933) has shown that the ventral nucleus of the medial geniculate body has a similar origin. Already in *Echidna* this process has been initiated for both nuclei.

The cerebral peduncles are peculiar in that they contain no representative of the fronto-pontine fibres of other mammals and that the pyramidal tracts lie exposed at their medial border. It has been emphazised that the substantia nigra is confined to the medial border of the peduncle in close association with the pyramid—a fact which accords with its supposed motor function. In the figures which HINES shows of this region in *Ornithorhynchus* the substantia nigra similarly lies at the medial border of the peduncle.

Schuster (1910) mapped the cortical pattern in *Echidna* and was unable to differentiate more than five areas (he does not describe the occipital region). The largest of these is area 3 which occupies the anterior two-thirds or more of the lateral surface of the hemisphere. Martin (1898) found that the electrically excitable cortex in *Ornithorhnychus* occupies the anterior two-thirds of the lateral aspect of the hemisphere. He emphasizes that there is very little localization, the whole area is diffusely excitable and only a laborious search enabled him to isolate vague regions for movements of the eyelids, face, and fore-limb. There is in *Ornithorhynchus* no cortical area anterior to the electrically excitable cortex : there is no frontal cortex. Area 3 in the cortex of *Echidna* is a similar diffuse region extending to the frontal pole. It is regarded by Kappers (1933) as the equivalent of the motor cortex of *Ornithorhynchus*, and that must be so for it is here that the pyramidal tracts arise. Further, area 3—according to Schuster's figures—is the only cortex in *Echidna* which contains anything like motor cells. So *Echidna*, like *Ornithorhynchus*, possesses no frontal area in the cortex. The resultant pyramidal tracts are ridiculously small for an area which occupies two-thirds of the lateral surface of the hemisphere, but as this region is the end-station of many thalamic radiations, it must represent a very diffuse sensory-motor area.

In the opossum Tsai (1925, *b*) has shown that the substantia nigra lies at the lateral border of the cerebral peduncle. Turner (1924) has extirpated the excitable cortex in the opossum and traced the resultant degeneration in the pyramidal tracts, and it is clear from his figures that the pyramidal tract in the opossum lies at the lateral border of the peduncle, as the situation of the substantia nigra would indicate. Therefore in the opossum, all of the cerebral peduncle except the pyramidal component has arisen from the hemisphere anterior to the motor cortex.

The experiments of Gray and Turner (1924) and of Rogers (1924) demonstrate that the excitable cortex in the opossum lies around the fissura orbitalis, but that it is confined especially to the area behind this. Gray, P. A. (1924) has further shown that this a discrete cortical area in front of which lies an equally discrete frontal area. This must be the site of origin of the non-pyramidal portion of the peduncle. Thus the peduncles in the opossum contain, besides pyramidal fibres, only the fronto-pontine components of the peduncles of higher mammals.

In *Echidna* there is no frontal cortex and consequently no fronto-pontine tract ; for *Ornithorhynchus* this seems also certain. The absence of fronto-pontine fibres is associated with an absence of any pretrigeminal development of the pons and with a diminutive condition of the lobus medius of the cerebellum. On the other hand, in association with large temporo- and occipito-pontine tracts there is a great retrotrigeminal development of the pons and a very large lobus anterius in the cerebellum.

In marsupials, with a discrete frontal cortex there is a large fronto-pontine tract in the peduncle, a purely pre-trigeminal development of the pons and a hypertrophied lobus medius in the cerebellum. With the absence of temporo- and occipito-pontine fibres in the peduncle there is a complete failure of development of any retro-trigeminal pons and a tiny lobus anterius in the cerebellum.

The conditions are clearly complementary. The temporo-occipital cortex sends its fibres to the caudal—or retro-trigeminal—part of the pons whence they are relayed to the lobus anterius of the cerebellum ; the frontal cortex sends its fibres to the frontal—or pre-trigeminal—part of the pons whence they are relayed to the lobus medius of the cerebellum.

Thus these remarkable features in the Monotreme brain—the enormous size of the lobus anterius of the cerebellum and the purely retro-trigeminal development of the pons—are the reflection of the absence of any frontal area in the cerebral cortex and consequent failure of development of a fronto-pontine tract in the cerebral peduncle.

It follows from such a comparative study that in higher animals with both fronto-pontine and temporo- and occipito-pontine tracts, and with a fully developed pons, impulses from the frontal cortex are projected on the lobus medius of the cerebellum, those from the temporo-occipital cortex on the lobus anterius.

The Hypothalamus

The Corpus Mamillare—This forms a large, unpaired body in which medial and lateral nuclei could be distinguished on each side. The cells are small and closely packed, and do not appear to be divisable into further sub-groups such as TSAI (1925, *b*) and HO-NIEN CHU (1932) describe for the opossum. The fornix is poorly defined and passes with some medial fore-brain fibres to the lateral nucleus, fig. 19. The peduncle of corpus mamillare arises from the lateral nucleus. From the medial nucleus arise the rudimentary fasciculus mamillo-thalamicus and the tractus mamillo-tegmentalis.

The Peduncle of the Corpus Mamillare—The peduncle is the largest fibre tract related to the mamillary body. It arises from the lateral nucleus and passes dorsally and caudally in a wide curve. This tract comes into close relation with the medial lemniscus and may give fibres to or receive them from the lemniscus. Despite its size, fig. 18, the peduncle is soon lost in the tegmentum. It was not possible to trace any fibres to the central grey matter which TSAI regards as their probable destination. The relation to the medial lemniscus is of interest in view of the fact that some authors have suggested the passage of gustatory fibres from the lemniscus to the mamillary body by way of the peduncle.

The Tractus Mamillo-Tegmentalis—This tract arises from the medial nucleus of the mamillary body and runs caudally with the peduncle of the corpus mamillare. Some of its fibres end in the ventral tegmental nucleus, the remainder pass on to the tegmentum. TSAI suggests that this tract also reaches the central grey matter, but that is not clear from these sections.

The Supra-Mamillary Decussation—This appears to be the same as the decussation described by ZIEHEN (1908) as " Schnopfhagen's crossing." It is of complex origin. Many of the fibres arise from the mamillary body itself, while a few come from the medial fore-brain bundle. The origin and destination of other components could not be ascertained, fig. 19.

The Fasciculus Mamillo-Thalamicus—In *Echidna* this tract has scarcely evolved beyond the reptilian condition and is extremely difficult to follow. The fibres arise from the medial nucleus of the corpus mamillare and pass forwards and dorsally close to the medial border of the medial fore-brain bundle, fig. 20. As they ascend, the scattered fibres pass medially to lie at the posterior border of the stria medullaris against which they appear to be crowded by the pressure of the ventral nucleus of the thalamus, fig. 22. The majority of these fibres end in the anterior poles of the ventro-medial and ventral thalamic nuclei while a few reach the lateral nucleus.

The Fornix—This is a very inconspicuous tract which can scarcely be distinguished at the medial side of the medial fore-brain bundle. It passes to the lateral nucleus of the mamillary body, fig. 20.

The Medial Hypothalamic and Preoptic Nuclei—These constitute a medial area rather than medial nuclei. The cells are small and scattered, and lie between the medial fore-brain bundle and the mid-line, fig. 21. A ventral hypothalamic nucleus was vaguely discernible. The medial hypothalamic and preoptic nuclei are continuous and combine to give origin to the medial olfacto-habenular component of the stria medullaris.

The Lateral Hypothalamic and Preoptic Nuclei—Like the former, these form one continuous cell mass. This lies amongst the fibres of the medial fore-brain bundle, fig. 21, and gives origin to the lateral olfacto-habenular component of the stria medullaris.

The Medial Fore-Brain Bundle—This is diffuse, and the fibres were so poorly stained that their exact origin and destination are uncertain. According to Tsai (1925, *b*) this tract in the opossum (his *tractus medialis telencephali*) receives fibres from the nucleus parolfactorius, the nucleus accumbens, the tuberculum olfactorium, the precommissural bundles of the stria terminalis, the nucleus of the diagonal band of Broca, and the preoptic region. He says that it is distributed in four main bundles : a tractus olfacto-hypothalamicus to the hypothalamus, a tractus olfacto-mamillaris to the corpus mamillare, a tractus olfacto-peduncularis to the ganglion interpedunculare, and a tractus olfacto-tegmentalis to the tegmentum. In these sections it is possible to discern that the bulk of the medial fore-brain bundle arises from the medial olfactory region of the hemisphere, fig. 22. As the fibres pass posteriorly they are distributed to the hypothalamus, the corpus mamillare and the tegmentum. Some cross in the supra-mamillary decussation but none could be traced to the interpeduncular ganglion. The fornix and the fasciculus mamillo-thalamicus are closely related to the medial side of this bundle.

The Nucleus Supra-Opticus—This nucleus lies in the anterior hypothalamic region, dorsal and lateral to the optic chiasma, fig. 21. It is quite discrete and contains small cells. No optic fibres appear to end here but it gives rise to some of the fibres which cross in the dorsal supra-optic commissure of Meynert.

Other Hypothalamic Connections—In addition to those described, large numbers of fibres reach the hypothalamus from various regions. A compact mass of fibres coming from the hemisphere to lie at the dorsal aspect of the medial fore-brain bundle was identified as the olfactory projection tract of CAJAL, fig. 21. Others come from the red nucleus (field H_2 of FOREL), medial lemniscus, the pretectal nucleus, the tectum, the posterior and ventro-medial nuclei of the thalamus and from other sources which could not be identified.

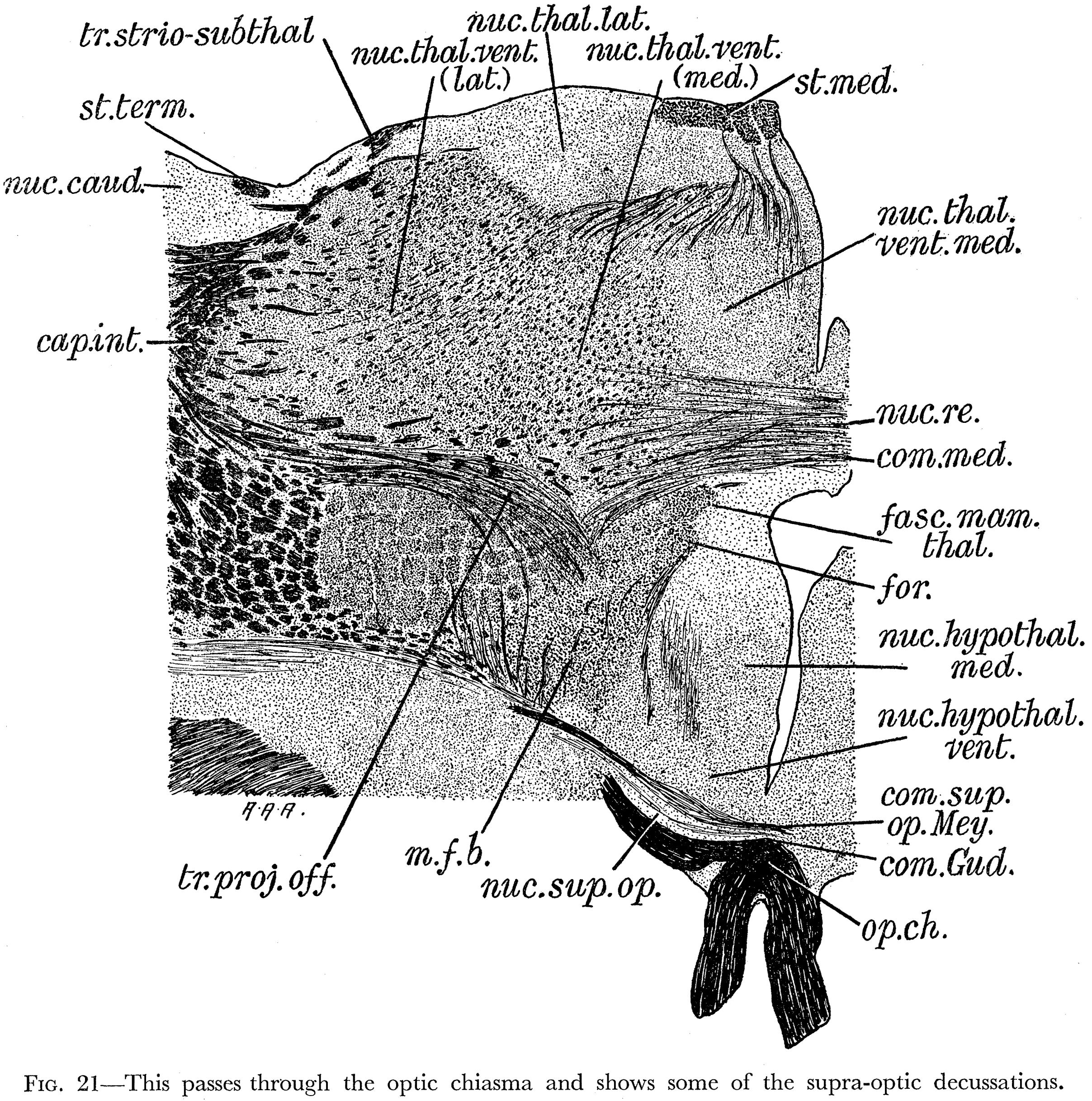

FIG. 21—This passes through the optic chiasma and shows some of the supra-optic decussations. The nucleus dorso-medialis can no longer be distinguished from the lateral nucleus of the thalamus. The ventral nucleus comprises chiefly pars lateralis. × 10.

THE SUPRA-OPTIC COMMISSURES

The Commissure of GANSER—This is definitely post-optic in position but is continuous anteriorly with the dorsal supra-optic commissure of MEYNERT. It thus justifies its association with this in GURDJIAN's (1927) classification. Laterally the fibres could be traced dorsally into the lateral hypothalamic nucleus and medial fore-brain bundle, but they could not be followed to the subthalamus as TSAI (1925, *b*) and GURDJIAN (1927) have described.

The Commissure of MEYNERT—This is a direct anterior continuation of the commissure of GANSER. The majority of the fibres come from the hemisphere, and especially from the corpus striatum, fig. 21. Other fibres arise from the lateral hypothalamic region and the nucleus supra-opticus, but connections with the medial geniculate body and the tectum, such as GURDJIAN describes for the rat, could not be found.

The Commissure of GUDDEN—The commissura transversa arises almost exclusively from the ventral nucleus of the medial geniculate body, fig. 16, but some fibres appear to come from the ventral nucleus of the lateral geniculate body. In view of the close connection between the superficial part of the inferior brachium and the ventral nucleus of the medial geniculate body, it is probable that fibres pass this way from the dorsal nucleus of the lateral lemniscus. This nucleus is the mammalian representative of the nucleus isthmi of amphibia, reptiles, and birds and many authors—JOUSTRA (1918), KAPPERS (1921), LARSELL (1924), HUBER and CROSBY (1926), and others—have described connections between the nucleus isthmi and the commissura transversa.

The commissure is well developed and is clearly not affected by the deficient state of the visual apparatus. The fibres pass ventrally and medially with the optic tract to cross as the ventral supra-optic decussation.

The Optic Chiasma—This is diminutive and the decussation is practically, if not entirely, complete. A very few of the most lateral optic nerve fibres may pass to the homolateral tract. A few fibres passing from the optic tracts through the cerebral peduncle represent the anterior and posterior accessory optic roots of BOCHENEK. None of these could be followed to the corpus subthalamicum, and no nucleus opticus tegmenti could be identified.

The hypothalamus in *Echidna* does not reveal many striking features. It is, indeed, very old phylogenetically, and very conservative throughout the vertebrate series. One peculiarity which links *Echidna* with the sub-mammalia, and is in sharp contrast to the majority of mammals, is the extremely poor development of the fasciculus mamillo-thalamicus. In this respect *Echidna* exhibits a close resemblance to the Sauropsida. DE LANGE (1913) describes a fasciculus mamillothalamicus in *Varanus*, and CAIRNEY (1926) a representative of this in *Sphenodon*, but HUBER and CROSBY (1926) were unable to find any definite fasciculus in the alligator and it seems certain that even if such a fasciculus is present in the Sauropsida it is usually so poorly differentiated from the general periventricular system that it is difficult to trace. In *Echidna* the corpus mamillare is very large, but its connections are chiefly with lower centres in the brain-stem. The connections with the fore-brain are small despite the fact that *Echidna* is usually regarded as macrosmatic. It may be that the large epithalamus supplements the fornix-mamillare-thalamic system for it has large hypothalamic and cortical components.

The Pars Dorsalis Diencephali

The Ventral Group of Nuclei—This, and especially the nucleus ventralis proper, is the most outstanding feature of the diencephalon in *Echidna*. Ziehen (1908) described a nucleus lateralis which corresponds to the combined nuclei ventralis and lateralis of this description. He also mentioned a nucleus dorso-medialis posterior which represents the nucleus dorso-medialis, and a nucleus " 1 " which is part of the nucleus ventralis medialis. For *Ornithorhynchus* Hines described a nucleus medialis corresponding to the nucleus ventralis medialis, and nuclei dorso-lateralis, medio-lateralis, and ventro-lateralis which correspond respectively to the lateral nucleus, and the medial and lateral parts of the ventral nucleus.

The ventral group of nuclei comprises, according to Le Gros Clark (1932, *b*), the nuclei ventralis and ventralis medialis, and the dorsal nuclei of the medial and lateral geniculate bodies.

The ventral nucleus in *Echidna* is enormously developed, but is smaller than that in *Ornithorhynchus* where the trigeminal nerve is so much larger. Posteriorly the ventral nucleus projects as the " pulvinar," anteriorly it reaches the anterior pole of the diencephalon and extends laterally into the hemisphere, compressing the internal capsule and corpus striatum, fig. 20. As the medial lemniscus is traced into the ventral nucleus, fig. 17, it is found that the lateral—non-trigeminal—half, or more, soon breaks up among the cells while the medial part persists unaltered. More anteriorly, fig. 18, the trigeminal part of the lemniscus enters the medial part of the ventral nucleus which is rendered conspicuous by the passage of the fibres. These two parts of the ventral nucleus are the pars lateralis and pars medialis respectively. The pars lateralis receives spinal impulses, the pars medialis trigeminal. The two parts are clearly separable by the more compact arrangement of the cells in the medial. Throughout their extent both nuclei send large numbers of fibres to the hemisphere, those from the medial part pass either through the lateral or ventral to it in the ventral medullary lamina, fig. 19. Posteriorly, in addition to lemniscal fibres, both nuclei receive fibres from the tectum and the nucleus pretectalis ; anteriorly, the combined nuclei receive a few mamillo-thalamic fibres, fig. 22. Fibres also pass from the pars medialis to the fasciculus retroflexus—tractus thalamo-epithalamicus—and both parts send fibres to the pars ventralis diencephali.

The nucleus ventralis medialis is very large, fig. 20. It extends caudally medial to the fasciculus retroflexus in the sub-habenular region, fig. 19, and

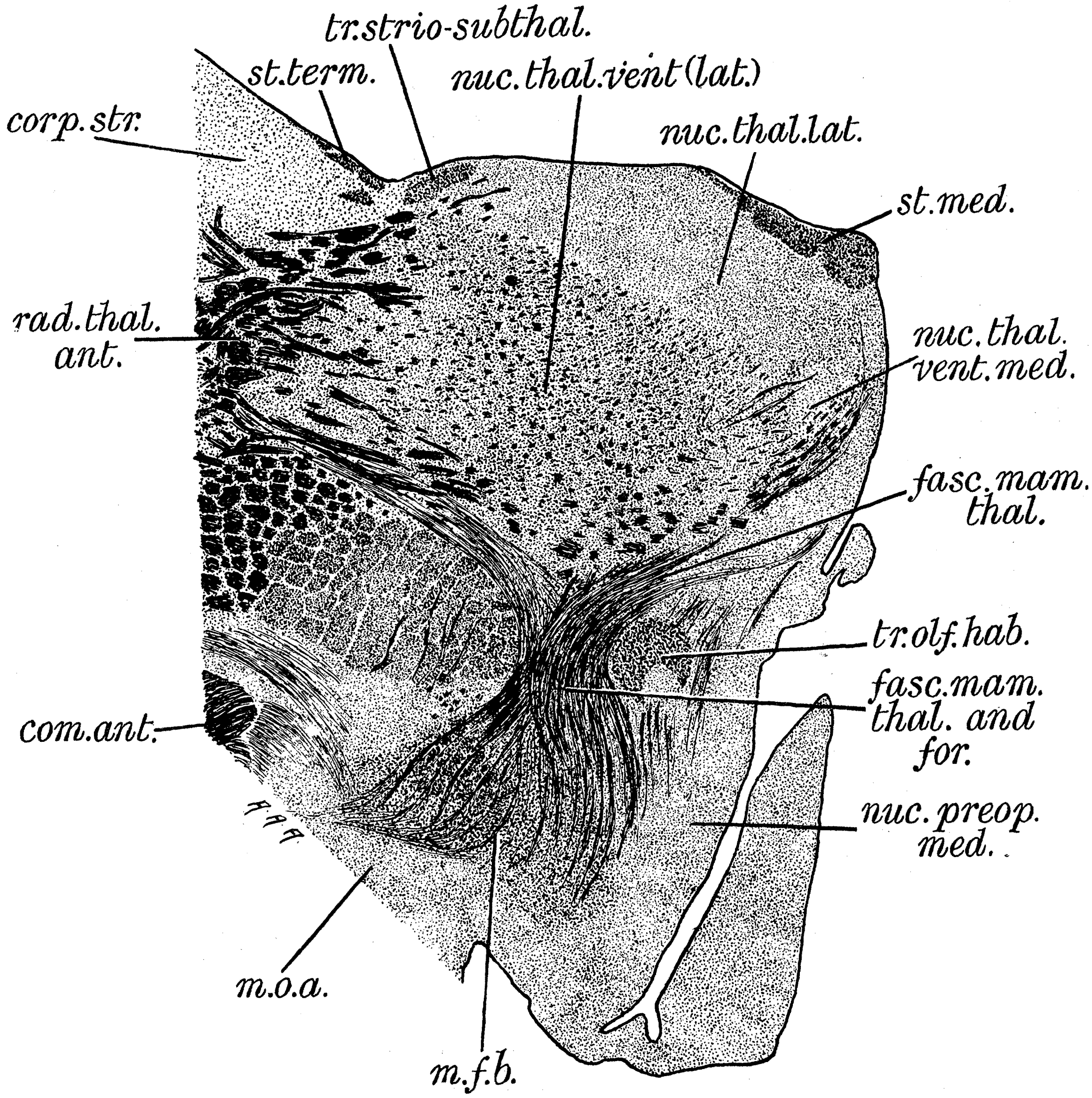

FIG. 22—In this section the fasciculus mamillo-thalamicus is entering the anterior poles of the nuclei ventralis medialis, ventralis, and lateralis. The large medial and lateral olfacto-habenular components of the stria medullaris are conspicuous in the preoptic region. The anterior commissure is approaching the mid-line. × 10.

anteriorly is continued in the nucleus antero-medialis to the anterior pole of the diencephalon. This combined nucleus receives no lemniscal contributions, but part of the mamillo-thalamic tract enters its anterior pole. The nucleus ventralis medialis has connections with the habenular nuclei, the tectum, the hypothalamus, and the hemisphere. The fibres to the hemisphere probably end in the corpus striatum as in other mammals. They pass through and ventral to the ventral nucleus. The nucleus ventralis medialis lies between the ventral nucleus and the periventricular grey matter and corresponds to the nucleus submedius of RIOCH (1931) in carnivora.

The dorsal nucleus of the medial geniculate body is identified by tracing the inferior brachium to the thalamus. The deep, thick auditory fibres end in the posterior part of the pars lateralis of the ventral nucleus, fig. 16. This represents the as yet barely differentiated dorsal nucleus of the medial geniculate body which is here an integral part of the ventral nucleus of the thalamus. LE GROS CLARK (1933) has shown that the dorsal nucleus of the medial geniculate body has evolved out of the general sensory or ventral nucleus ; in *Echidna*, with the first improvement in the auditory mechanism, the process of differentiation has just commenced. The auditory radiations cannot be separated with certainty from the optic and posterior thalamic radiations, all pass together to the posterior part of the hemisphere—area 4 of SCHUSTER.

The dorsal nucleus of the lateral geniculate body is identified by tracing optic fibres. These pass through the ventral nucleus to reach the posterior pole of the ventral nucleus of the thalamus, fig. 16. The dorsal nucleus of the lateral geniculate body is better differentiated than that of the medial to which it lies posterodorsal and lateral. KAPPERS (1921) and LE GROS CLARK (1932, *a*) have shown that the dorsal nucleus of the lateral geniculate body is derived from the ventral nucleus of the thalamus ; it is seen here in an early stage of separation although the condition is exaggerated, no doubt, by the generally poor visual development. Some optic fibres can be traced over the lighter cell mass dorsal to the dorsal nucleus of the lateral geniculate body, fig. 16. These appear to be purely mesencephalic fibres, but their presence led ZIEHEN to regard the two parts together as the dorsal nucleus which he called the *nucleus zonale*. It is extremely doubtful whether any optic fibres end in the clearer portion, however, and, poorly differentiated as it is, it certainly represents the true pulvinar thalami of higher mammals. The optic radiations pass with the auditory to the posterior part of the cerebral cortex.

The Lateral Group of Nuclei—Typically this group comprises the nuclei lateralis, dorso-medialis and suprageniculatus, and the pulvinar. In *Echidna*, all except the nucleus suprageniculatus were identified. The group as a whole is distinguished by its lack of lemniscal connections, its very scattered cell composition and lighter staining. It forms a continuous thin layer dorsal to the ventral group and, in keeping with the primitive condition of the higher association areas of the cortex, is poorly differentiated from the ventral nuclei.

The lateral nucleus is the largest of this group. It extends over the whole of the dorsal surface of the ventral nucleus, and especially the pars lateralis, and the actual boundary line between the two is almost beyond definition, fig. 19. The cells of the pars lateralis merely become more sparse and lighter stained, and lemniscal fibres fail. The lateral nucleus is clearly a portion of the lateral part of the ventral nucleus and is slowly differentiating to assume its higher functions. The lateral nucleus receives fibres from the tectum and the nucleus pretectalis, and is intimately related to the lateral part of the ventral nucleus. It sends fibres with the thalamic radiations to the cortex.

The nucleus dorso-medialis can only be identified with certainty in the caudal part of the thalamus, anteriorly it merges with the lateral nucleus. Its relation to the pars medialis of the ventral nucleus is exactly the same as that of the lateral nucleus to the pars lateralis. It has clearly arisen from the pars medialis. The close relation which this nucleus always holds to the trigeminal portion of the ventral nucleus of the thalamus is emphasized by the fact that some authors have described it as the end-station for trigeminal fibres. Its fibres pass to the cortex with those of the pars medialis.

The pulvinar bears the same relation to the dorsal nucleus of the lateral geniculate body as do the other members of this group to their own parent nuclei. It is a barely separated portion of the dorsal nucleus of the lateral geniculate body but receives no optic fibres. Anteriorly it is incompletely defined from the lateral nucleus by cortico-tectal fibres, fig. 16—a typical relation. As in other mammals the pulvinar receives tectal and pretectal fibres, and the mesencephalic optic root runs over its surface. Its own radiations pass with those of the two geniculate bodies to the posterior part of the cortex.

No discrete nucleus suprageniculatus was defined, but the close relation which the pulvinar bears to the dorsal nucleus of the medial geniculate body, and the close association of the cortical radiations of the two, make it probable that the nucleus suprageniculatus finds representation in the cell mass described here as the pulvinar.

The Anterior Group of Nuclei—The fasciculus mamillo-thalamicus is so rudimentary that its influence is not sufficient to evoke the differentiation of a separate group of anterior nuclei. However, since the fasciculus mamillo-thalamicus is definable, it is possible to trace its fibres to the precursors of the anterior nuclei. When this is done, fig. 22, it is found that the majority of the fibres end in the anterior poles of ventro-medial and ventral nuclei, and that a very few reach the anterior end of the nucleus lateralis. These must represent the nuclei antero-medialis, antero-ventralis, and antero-dorsalis respectively. Their connections are the same as those of the main nuclei from which they have not yet separated : the ventro-medial nucleus with the corpus striatum, the ventral and lateral nuclei with the cortex.

The Mid-Line Nuclei—The great expansion of the ventral nucleus has so distorted the general configuration of the pars dorsalis diencephali that most of these have been crushed aside almost beyond recognition. It is possible to distinguish a nucleus reuniens, a nucleus centralis medialis, nuclei centrales laterales, and a nucleus parafascicularis.

The nucleus reuniens lies among the fibres of the commissura media, fig. 20. The nucleus centralis medialis lies in the massa intermedia dorsal to the commissura media and is continued laterally in the nuclei centrales laterales. The nucleus parafascicularis lies along and lateral to the fasciculus retroflexus, fig. 19.

The Commissura Media—Hines described a similar commissure in *Ornithorhynchus*. She stated that its chief connections were with the corpus striatum and called it the *commissura thalami*. As Ziehen showed, this commissure carries chiefly thalamic fibres. It receives some from the corpus striatum and, since it acquires others from the tectum, it must be considered homologous in part with the tractus tecto-reuniens of the alligator. The nucleus reuniens lies among the fibres, fig. 20.

THE EPITHALAMUS

The habenular ganglion contains the usual medial and lateral nuclei, fig. 19. The cells of both are similar in type but those of the medial nucleus are very closely packed. The ganglion as a whole is very large and extends well anteriorly with the stria medullaris. Fibres enter the ganglion from the pretectal nucleus, the medial part of the ventral nucleus of the thalamus, the nucleus ventralis medialis, both striæ medullares and the opposite habenular ganglion. A few appear to reach it from the pineal stalk. Fibres pass from the ganglion to the striæ medullares, and to the ganglion interpedunculare by the fasciculus retroflexus.

The pineal body is a hollow globular organ of glandular structure, fig. 17. It appears to have fibre connections with the habenular ganglia. Unfortunately, it was missing from the gross specimens.

The habenular commissure lies in the dorsal part of the pineal stalk, fig. 18. It interconnects the two habenular ganglia and transmits fibres from the striæ medullares.

The striæ medullares are considerable fibre tracts which encircle three-quarters of the medial border of the diencephalon. They appear to supplement the rudimentary fasciculi mamillo-thalamici. The major part of each stria comes from the hypothalamic and preoptic regions. In the hypothalamus the fibres rise from far back and a transverse section through the front of the diencephalon cuts them twice, fig. 22. The components from the medial and lateral preoptic and hypothalamic regions are the medial and lateral olfacto-habenular tracts respectively. Contributions from the fornix contain cortico-habenular components, while some fibres arise from the medial olfactory region independent of the fornix and a few appear to come directly from the stria terminalis. As mentioned above, a well-marked tract—the tractus thalamo-epithalamicus—arises from the pars medialis of the ventral nucleus of the thalamus and passes along the fasciculus retroflexus to join the stria medullaris, fig. 19.

It is generally considered that the nucleus rotundus of the Sauropsida is homologous with part of the ventral nucleus of the mammalian thalamus. KAPPERS (1921), HUBER and CROSBY (1929, *a*), INGVAR (1923), and LE GROS CLARK (1932, *a*) have all emphasized this. WALLENBERG (1904) traced lemniscal fibres to the nucleus rotundus in the dove, DE LANGE (1913) followed trigeminal fibres to the same nucleus in *Varanus*, and HUBER and CROSBY (1926) considered it probable that trigeminal fibres reach this nucleus in the alligator. There seems little doubt that trigeminal fibres reach the nucleus rotundus in Sauropsida. In *Echidna* the pars medialis of the ventral nucleus is the end-station of the trigeminal fibres and it corresponds closely with the nucleus rotundus in its topographical relations to the fasciculus retroflexus. It seems certain that it is the homologue of the Sauropsidan nucleus rotundus.

The only possible homologue of the pars lateralis of the ventral nucleus is the *nucleus dorso-lateralis anterior* described by HUBER and CROSBY (1926) for the alligator. This nucleus extends from the anterior pole of the diencephalon almost to its posterior extremity and is composed of the same type of cells as the nucleus rotundus. The posterior end of the nucleus dorso-lateralis anterior shows a definite differentiation of its cells to receive optic tract fibres and HUBER and CROSBY regard this as the probable forerunner of the dorsal nucleus of the lateral geniculate body. The anterior end of this nucleus in *Sphenodon* according to CAIRNEY (1926), and of its representative in *Varanus* according to DE LANGE (1913), receives mamillo-thalamic fibres. In *Echidna* the anterior part of the pars lateralis of the ventral nucleus receives mamillo-thalamic fibres, and from its posterior end there is a differentiation of cells which receives optic tract fibres. (There is, in addition, a differentiation of cells for the reception of auditory and spinal lemniscal fibres, but such has not been described for sub-mammalia.)

Thus in *Echidna* the nucleus antero-ventralis, the pars lateralis of the ventral nucleus and the dorsal nuclei of the medial and lateral geniculate bodies form one continuous cell mass which is strikingly similar to the nucleus dorso-lateralis anterior of the alligator and there is no doubt that the two are homologous.

In higher mammals the dorsal nuclei of the geniculate bodies and the nucleus antero-ventralis become separated from the pars lateralis. What remains of this joins the nucleus rotundus—pars medialis—to form the typical mammalian ventral nucleus of the thalamus. But despite the much smaller trigeminal nerve, trigeminal fibres are always described as passing to the medial part of the ventral nucleus.

The nucleus ventralis medialis is also phylogenetically old. It is distinguished by its lack of lemniscal connections. In many mammals (LE GROS CLARK, 1932, *b*) this nucleus is continuous with the nucleus antero-medialis ; in *Echidna* this is obvious. Posteriorly the nucleus ventralis medialis extends into the sub-habenular region medial to the fasciculus retroflexus. The fibre connections are chiefly with the corpus striatum. The *nucleus dorso-medialis anterior* in the alligator bears exactly the same relations. It extends from the anterior pole of the diencephalon, where, according to HUBER and CROSBY and DE LANGE, it receives the equivalents of mamillo-thalamic fibres, to the sub-habenular region medial to the fasciculus retroflexus. Further, its connections are almost entirely with the corpus striatum. The sauropsidan nucleus dorso-medialis anterior is clearly the precursor of the combined nuclei antero-medialis and ventralis medialis in mammals. In higher mammals the nucleus antero-medialis frequently separates as a distinct end-station for mamillo-thalamic fibres while the remaining nucleus ventralis medialis tends to become progressively smaller. It is sometimes called the nucleus submedius.

LE GROS CLARK (1929), recognized the homology of the nucleus antero-medialis with the nucleus dorso-medialis anterior, but he suggested (1932, *b*) that the nucleus ventralis medialis is the homologue of the nucleus rotundus. The absence of lemniscal connections renders this very unlikely. (In a private communication Professor LE GROS CLARK informed me that the homology was advanced very tentatively, and that he regards it as doubtful.)

Little more need be said concerning the anterior nuclei. In mammals there are typically three : antero-medialis, antero-ventralis, and antero-dorsalis. These have been described by many authors—GURDJIAN (1927), RIOCH (1931), LE GROS CLARK (1929), and others. It has already been shown that in accordance with the poor development of the fasciculus mamillo-thalamicus, the anterior nuclei have not yet separated from their parent bodies. The nucleus antero-medialis is contained within the nucleus dorso-medialis anterior of Sauropsida and in *Echidna* and many other mammals never separates from the nucleus ventralis medialis. The nucleus antero-ventralis is part of the nucleus dorso-lateralis anterior in the alligator and in *Echidna* still lies within the lateral part of the ventral nucleus ; but in most other mammals it separates as a discrete nucleus. The nucleus antero-dorsalis is on a different footing to the other two. As LE GROS CLARK says, it has no reptilian representative. In *Echidna* it lies within the lateral nuclear group, but is certainly a differentiated portion of the precursor of the nucleus antero-ventralis. In higher mammals the nucleus antero-dorsalis separates from the lateral nucleus, and in *Macroscelides* and the rodents assumes relatively enormous proportions (LE GROS CLARK). The connections of the anterior nuclei are the same as those of their parents. The nucleus antero-medialis appears to have connections with the corpus striatum, the representatives of the antero-ventral and antero-medial nuclei are related to the cortex ; according to LE GROS CLARK and BOGGON (1933), they are connected to the cingular area of the cortex in higher mammals.

If any representative of the lateral nuclei exists in sub-mammalia it is so small that it has hitherto remained undescribed. They are essentially a mammalian characteristic and their evolution proceeds in harmony with that of the association areas of the neopallium. Their rudimentary condition in *Echidna*, however, serves the useful purpose of demonstrating their mode of origin.

Just as the association areas in the cerebral cortex have developed from the receptive areas, so in the thalamus the first representatives of the lateral group of nuclei have evolved from the discrete receptor nuclei. The lateral group of nuclei does not contain one nucleus which sends extensions to the medial geniculate body, the lateral geniculate body, the ventral nucleus, and the antero-ventral nucleus ; it is a complex of several nuclei each of which has arisen independently *in situ* from its own receptor element. Thus the pulviner is an intrinsic part of the dorsal nucleus of the lateral geniculate body and its apparent separation is the result of its growth in response to the demands of the association area with which it is related, and with which it is evolving. Similarly, the lateral nucleus is a part of the non-trigeminal element of the ventral nucleus, the nucleus dorso-medialis of the trigeminal element ; the nucleus suprageniculatus is part of the dorsal nucleus of the medial geniculate body and the nucleus antero-dorsalis of the nucleus antero-ventralis.

It is well known that the essential units of the lateral nuclei are phylogenetically ancient as far as the mammals are concerned. In a primitive mammal like *Echidna* they lie close together immediately related to the receptor nuclei. Growth of the thalamus is not expressed in the expansion of the original units of the lateral nuclei but in the interposition of new thalamic elements between them. Thus in an ascending phylogenetic scale these units are progressively forced apart by the appearance of even higher physiological levels within the thalamus.

Echidna affords an excellent example of Elliot Smith's (1910) conception of a primitive mammal whose thalamic radiations are topographically projected upon the most adjacent cortical area. The fibres from the posterior part of the thalamus end in the occipital region, those from the centre in the middle of the hemisphere and those from the anterior part in the frontal area. With the projection fibres from the receptor nuclei of the thalamus pass the projection fibres from the associated units of the lateral nuclei. The sensory fibres end in the simple sensory projection areas, the companion association fibres in the surrounding association areas. Each individual receptor unit in the thalamus has evolved its own higher physiological level, in the cortex the same thing has occurred ; the processes in both are mutually interdependent. As an expression of this the association fibres from the higher level in the thalamus always accompany the sensory projection fibres and this primitive relation is maintained throughout the mammalian series.

As evolution progresses the simple arrangement in *Echidna* becomes obscured by the development of even higher physiological levels. The primitive area striata and its surrounding area parastriata are pushed further from the primitive tactile and auditory areas and their simple association cortex by the interposition of yet higher levels—peristriate area and so on. Then these secondary areas are separated by the intervening formation of the visuo-auditory and visuo-sensory bands of Elliot Smith (1907). Finally, the great expansion of the frontal cortex overshadows all previous achievements and stamps the brain with humanity.

Every step in the progress of cortical evolution is accompanied by a similar step in thalamic evolution. When the secondary association areas appear in the cortex secondary association nuclei arise between the lateral thalamic nuclei and push the primary elements apart. Tertiary association nuclei separate them still further and the mass progressively enlarges by the successive interposition of higher elements until the great thalamus of Man with its characteristic complexity emerges.

Throughout this process the primitive ground plan is never lost. The expansion distorts the picture but the primary association nuclei—pulvinar, nucleus suprageniculatus, nuclei lateralis, and dorso-medialis—maintain their connection with their receptive parent nuclei. The last stage in thalamic evolution is characterized by the growth of the centre median and dorso-medial nuclei. Le Gros Clark says (1932, *b*, p. 463) that the centre median nucleus " ....may be regarded therefore as an integrating mechanism related to that part of the thalamus in which progressive differentiation and growth are most obtrusive in the higher primates." The dorso-medial nucleus is related to the final evolution of the prefrontal cortex and serves to correlate the visceral mechanism of the hypothalamus with the highest cerebral centres.

CONCLUSIONS

While typically mammalian in its chief features, the brain of *Echidna* exhibits many very primitive traits. At the same time it presents striking specializations, some of which are distinct anticipations of some of the highest degrees of cerebral evolution.

The motor system is, on the whole, primitive. Part of the nucleus ambiguus retains a dorsal situation with the hypoglossal nucleus, and the facial nucleus has not yet attained its lowest level of ventral migration. The pyramidal tracts are very small and end in direct relation to the motor cells. They represent the direct pyramidal tracts only of higher mammals.

The sensory connections are extraordinarily well developed. The trigeminal apparatus is greatly hypertrophied, but the spinal sensory system is not inferior in importance. Trigeminal connections form the basis of the whole pontine-trapezoid-external arcuate fibre system and, in addition, are responsible for the great size of the paraflocculi in the cerebellum. The enormous expansion of the ventral nucleus of the thalamus, and its differentiation into medial and lateral portions, is due to the hypertrophy of the trigeminal and spinal sensory systems.

The scanty development of the cochlear connections reveals that they are being imposed upon an older vestibular mechanism. The cochlear apparatus makes use of these primitive pathways as far as the mid-brain, thereafter it exhibits its individuality in its direct passage to the medial geniculate body. It is doubtful whether many true auditory fibres are interrupted in the mid-brain ; it is equally doubtful if any vestibular impulses reach the fore-brain without such interruption. A dorsal nucleus of the medial geniculate body is just commencing to differentiate from the ventral nucleus of the thalamus.

The cerebellum reveals a high degree of specialization in the great size of the lobus anterius and the primitive state of the lobus medius. These are related to the purely retro-trigeminal development of the pons and the absence of fronto-pontine fibres in the peduncles. The paraflocculus is very large as a result of its extensive trigeminal support.

It is considered that the pons, corpus trapezoideum, and external arcuate fibres form part of a single system which has been laid down on a trigeminal foundation. This is subsequently permeated by vestibular elements. A further localized infiltration by cochlear fibres results in the appearance of the corpus trapezoideum.

The cerebral peduncles are large, but are peculiar in their lack of fronto-pontine tracts. This is the exact opposite of the condition in all other primitive mammals (excluding *Ornithorhynchus*), and is the result of the failure of development of any frontal cortex. In the peduncles run the temporo-trigeminal tracts which appear to be peculiar to *Echidna*. They serve to relate the fore-brain with the hind-brain and cerebellum, but are much more intimately associated with the trigeminal apparatus than with the vestibular.

The pars ventralis diencephali is, in most respects, typically developed. But the rudimentary condition of the fornix-mamillare-thalamic system forms a definite link with the Sauropsida. The corpus mamillare is much more effectively connected with the mid-brain than with the fore-brain.

The pars dorsalis diencephali is extremely primitive. Despite the hypertrophy of the ventral nucleus, a lateral group of nuclei is hardly differentiated. Representatives of most of these can be found, however, and they reveal that they have independently evolved from the individual receptor stations of the ventral nucleus. The atrophic condition of the visual system is reflected in the retention of the dorsal nucleus of the lateral geniculate body within the ventral nucleus of the thalamus ; the similar retention of the dorsal nucleus of the medial geniculate body reveals the origin of both. No discrete anterior nuclei have yet appeared, the rudimentary fasciculus mamillo-thalamicus cannot exert sufficient influence to provoke their differentiation from the main thalamic nuclei. The condition in *Echidna* provides a clue to the evolution of the mammalian thalamus from the Sauropsidan. The nucleus rotundus appears to be represented in the medial part of the ventral nucleus. The nucleus dorso-lateralis anterior has given rise to the nucleus antero-ventralis, the dorsal nuclei of the medial and lateral geniculate bodies and the lateral part of the ventral nucleus. The nucleus dorso-medialis anterior is represented in the nuclei antero-medialis and ventralis medialis.

The epithalamus is highly developed. It receives a well-marked contribution of fibres from the pars medialis of the ventral nucleus of the thalamus. This provides a basis for the intracerebral correlation of trigeminal and olfactory impulses.

The pars intercalaris encephali in *Echidna* is very large, but it is diffuse and lacks the elaborate differentiation seen in sauropsida. The growth of the hemispheres is diminishing the importance of this region which in higher mammals becomes relegated to a very subordinate position.

In nearly every marked cerebral peculiarity *Echidna* reveals its close relationship to *Ornithorhynchus* and emphasizes the isolated position of both animals. Except for the greater hypertrophy of the trigeminal system in *Ornithorhynchus*, and the presence of the tractus temporo-trigeminalis in *Echidna*, the brains of both are comparable point for point. The specializations of one are equally marked in the other ; where one exhibits some primitive feature the other is correspondingly retarded. Study of the brain confirms the view that the Monotremes are closely related and are widely divergent from the direct line of mammalian evolution.

ABBREVIATIONS USED IN FIGURES

aq., aqueduct of SYLVIUS.
*asc.*viii., ascending vestibular root.
*asc.n.*vii., ascending limb of seventh nerve.
brach.conj., brachium conjunctivum.
brach.inf., brachium inferius.
brach.inf.deep., deep part of inferior brachium.
brach.inf.super., superficial part of inferior brachium.

brach.po., brachium pontis.
brach.sup., brachium superius.
can.cent., central canal.
cap.int., internal capsule.
cer.ped., cerebral peduncle.
col.inf., inferior colliculus.
col.sup., superior colliculus.
com.ant., anterior commissure.
com.ant.c., anterior commissure of spinal cord.
com.col.inf., commissure of inferior colliculus.
com.col.sup., commissure of superior colliculus.
*com.*Gud., commissure of Gudden.
com.hab., habenular commissure.
com.hip., hippocampal commissure.
com.med., middle commissure.
com.post., posterior commissure.
com.post.c., posterior commissure of spinal cord.
*com.sup.op.*Mey., supraoptic commissure of Meynert.
cop.pyr., copula pyramidis.
corn.ant., anterior horn of spinal cord.
corp.mam., mamillary body.
corp.pin., pineal body.
corp.rest., corpus restiforme.
corp.str., corpus striatum.
corp.subthal., corpus subthalamicum.
corp.trap., corpus trapezoideum.
cul., culmen.
dec., declive.
dec.aud.dors., dorsal auditory decussation (of von Monakow).
dec.aud.inter., intermediate auditory decussation (of Held).
dec.brach.conj., decussation of brachia conjunctiva.
dec.fasc.ret., decussation of fasciculi retroflexi.
*dec.*For., decussation of Forel.
dec.lem.lat.vent., ventral decussation of lateral lemniscus.
*dec.*Mey., decussation of Meynert.
dec.pyr., pyramidal decussation.
dec.sens., decussating sensory fibres.
dec.sens.v., trigeminal sensory decussation.
dec.sup.mam., supramamillary decussation.
dec.tr.temp.v., decussation of temporo-trigeminal tracts.
des.v., descending root and nucleus of fifth nerve.
des.viii., descending vestibular root and nucleus.
dien.dors., pars dorsalis diencephali.
dors.sec.v., dorsal secondary trigeminal fibres.
em.ol., eminentia olivaris.
fasc.long.med., medial longitudinal fasciculus.
fasc.mam.thal., fasciculus mamillo-thalamicus.
fasc.ret., fasciculus retroflexus.
fasc.solit., fasciculus solitarius.
fib.arc.ext., external arcuate fibres.

fib.arc.int.dors., dorsal internal arcuate fibres.
fib.arc.int.vent., ventral internal arcuate fibres.
fib.cort.tect., cortico-tectal fibres.
fib.V.cereb., trigeminal fibres passing to cerebellum.
fib.V.tect., trigeminal fibres passing to tectum.
fib.op.sec., secondary optic fibres.
fib.pyr., pyramidal fibres.
fib.tect.thal., tecto-thalamic fibres.
fis.paraf., fissura parafloccularis.
fis.prepy., fissura præpyramidalis.
fis.pri., fissura prima.
fis.sec., fissura secunda.
fis.uv.nod., fissura uvulo-nodularis.
floc., flocculus.
for., fornix.
*for.*Mon., foramen of Monro.
fun.post., posterior funiculus of spinal cord.
Gan.*b.*, Ganser's bündel.
gang.hab., habenular ganglion.
gang.inter., interpeduncular ganglion.
gen.lat., lateral geniculate body (dorsal and ventral nuclei).
gen.med., medial geniculate body (dorsal and ventral nuclei).
glob.pal., globus pallidus.
hyp., hypophysis.
H.*H*1.*H*2, fields of Forel.
inf., infundibulum.
lem.lat., lateral lemniscus.
lem.med., medial lemniscus.
lem.v., trigeminal lemniscus.
ling., lingula.
lob.cent., lobulus centralis.
mas.inter., massa intermedia.
m.f.b., medial forebrain bundle.
m.o.a., medial olfactory area.
n.iii., oculomotor nerve.
n.iv., trochlear nerve.
n.v., trigeminal nerve.
n.vi., abducens nerve.
n.vii., facial nerve.
n.viii., eighth nerve.
n.ix., glossopharyngeal nerve.
n.x., vagus nerve.
n.xi., accessory nerve.
n.xii., hypoglossal nerve.
n.cer.i., first cervical nerve.
n.coch., cochlear nerve.
n.op., optic nerve.
n.vest., vestibular nerve.
nod., nodule.
nuc.iii., oculomotor nucleus.

nuc.iv., trochlear nucleus.
nuc.v.des., nucleus of descending fifth root.
nuc.v.mesen., mesencephalic root and nucleus of trigeminal nerve.
nuc.v.mot., motor nucleus of trigeminal nerve.
nuc.v.sens., sensory nucleus of trigeminal nerve.
nuc.vi., abducens nucleus.
nuc.vi.acc., accessory abducens nucleus.
nuc.vii., facialis nucleus.
nuc.vii.dors., dorsal anterior extension of facialis nucleus.
nuc.x.dors., dorsal vagal cell column.
nuc.xii., hypoglossal nucleus.
nuc.xii.l., lateral extension of hypoglossal cell column (vagal).
nuc.amb., nucleus ambiguus.
nuc.arc., nucleus arcuatus.
nuc.arc.v., nucleus arcuatus trigemini.
nuc.caud., nucleus caudatus.
nuc.cent.lat., nucleus centralis lateralis.
nuc.cent.med., nucleus centralis medialis.
nuc.cereb.lat., nucleus cerebelli lateralis.
nuc.coch.dors., dorsal cochlear nucleus.
nuc.coch.vent., ventral cochlear nucleus.
nuc.col.inf., nucleus of inferior colliculus.
*nuc.*Deit., nucleus of Deiters.
nuc.gr.cun., combined gracile and cuneate nuclei.
nuc.hab.lat., lateral habenular nucleus.
nuc.hab.med., medial habenular nucleus.
nuc.hypothal.med., medial hypothalamic nucleus.
nuc.hypothal.vent., ventral hypothalamic nucleus.
nuc.inter., nucleus intercalatus of Staderini.
nuc.op.tr., large-celled nucleus of optic tract.
nuc.po., nucleus pontis.
nuc.preop.med., medial preoptic nucleus.
nuc.pretect., nucleus pretectalis.
nuc.raph., nucleus of raphe.
nuc.re., nucleus reuniens.
nuc.ret., nucleus reticularis of cerebral peduncle.
nuc.ret.lat., lateral reticular nucleus of medulla oblongata.
nuc.rub., red nucleus.
nuc.subthal.med., medial subthalamic nucleus.
nuc.sup.op., nucleus supraopticus.
nuc.teg.dors., dorsal tegmental nucleus.
nuc.teg.vent., ventral tegmental nucleus.
nuc.thal.dors.med., dorso-medial nucleus of thalamus.
nuc.thal.lat., lateral nucleus of thalamus.
nuc.thal.post., posterior nucleus of thalamus.
nuc.thal.vent.(*lat.*), pars lateralis of ventral nucleus of thalamus.
nuc.thal.vent.(*med.*), pars medialis of ventral nucleus of thalamus.
nuc.thal.vent.med., nucleus ventralis medialis of thalamus.
nuc.vent.lem.lat., ventral nucleus of lateral lemniscus.
nuc.vest.p., principal vestibular nucleus.

ob., obex.
ol.inf., inferior olive.
ol.sup.lat., lateral part of superior olive.
ol.sup.med., medial part of superior olive.
op.ch., optic chiasma.
op.tr., optic tract.
paraf., paraflocculus.
ped.corp.mam., peduncle of corpus mamillare.
ped.ol.sup., peduncle of superior olive.
pin.rec., pineal recess.
po., pons.
"*pul.*," apparent pulvinar thalami.
pul.thal., true pulvinar thalami.
pyr., pyramid.
pyr.vii., facialis pyramid.
rad.op.aud., optic and auditory radiations.
rad.thal.ant., anterior thalamic radiations.
rad.thal.post., posterior thalamic radiations.
ros.po., rostum pontis.
st.med., stria medullaris.
st.term., stria terminalis.
str.gris.inter., stratum griseum intermedium.
str.gris.prof., stratum griseum profundum.
str.gris.super., stratum griseum superficiale.
str.med.inter., stratum medullare intermedium.
str.med.prof., stratum medullare profundum.
str.med.super., stratum medullare superficiale.
str.zon., stratum zonale.
sub.gel., substantia gelatinosa ROLANDI.
sub.nig., substantia nigra.
sul.ant.med., sulcus antero-medialis.
tect., tectum mesencephali.
tr.olf.hab., medial and lateral olfacto-habenular tracts.
tr.proj.olf., olfactory projection tract of CAJAL.
tr.pyr., pyramidal tract.
tr.strio-subthal., tractus strio-subthalamicus.
tr.tect.bulb., tractus tecto-bulbaris.
tr.tect.cereb., tractus tecto-cerebellaris.
tr.tect.spin., tractus tecto-spinalis.
tr.teg.ped., tractus tegmento-peduncularis.
tr.temp.v., tractus temporo-trigeminalis.
tr.thal.epithal., tractus thalamo-epithalamicus.
tub., tuber.
tub.v., tuberculum quinti.
tub.gr.cun., gracile-cuneate tubercle.
uv., uvula.
vel.med.ant., anterior medullary velum.
vent.iii., third ventricle.
vent.iv., fourth ventricle.
z.i., zona incerta.

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