PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Primitive Features of the Cerebrum, with Special Reference to the Brain of the Bushwoman Described by Marshall

Joseph L. Shellshear

Phil. Trans. R. Soc. Lond. B 1934 **223**, 1-26
doi: 10.1098/rstb.1934.0001

PHILOSOPHICAL TRANSACTIONS.

I. *The Primitive Features of the Cerebrum, with Special Reference to the Brain of the Bushwoman described by* MARSHALL.

By JOSEPH L. SHELLSHEAR, *D.S.O., M.D., University of Hong Kong.*

(*Communicated by* G. ELLIOT SMITH, *F.R.S.*)

(Received July 3, 1933. Read November 2, 1933.)

[PLATES 1–3.]

In 1864 JOHN MARSHALL, of University College Hospital, London, published in the Philosophical Transactions' an account of a brain of exceptional interest, that of a Bushwoman. The original documents and photographs relating to this brain were recently handed to Professor ELLIOT SMITH by his daughter, Miss MARSHALL, On his advice these documents have been studied anew.* In making his drawings from these photographs the lithographer made some slight changes which convey an erroneous impression of the primitive features that confer exceptional importance on this Bushwoman's brain. The progress of knowledge of this subject since 1864 enables us to interpret the photographs in another way and so make this interesting evidence available for the interpretation of such archaic forms of brain as are revealed in the endocranial casts of *Pithecanthropus*, *Sinanthropus*, and *Eoanthropus*. The original photographs represent the dorsal, ventral, lateral, anterior and posterior aspects of both hemispheres and the medial aspect of the left hemisphere. There is no photograph of the medial aspect of the right hemisphere. In addition to the photographs of the brain there are photographs of the head before the removal of the brain, and fortunately a photograph of the left hemisphere *in situ* within the cranium. MARSHALL'S photographs are exactly the same size as the lithographic figures; and he states that the figures agree in size with the preserved brain. He also gives measurements of the cerebrum taken from intracranial casts. There is a small discrepancy between the length of the cerebrum as measured on the photograph showing the brain in the cranium and the figures in his table. The amount of shrinkage is shown in fig. 25, Plate 3. In estimating the form and size of the outline of the endocranial cast of the Bushwoman figured in this paper, MARSHALL'S maximum figures are taken; allowing for this possible error, his illustrations enable us to reproduce the form fairly accurately. In

* Professor SHELLSHEAR searched in vain for the actual brain in the museums of University College, University College Hospital, and the Royal College of Surgeons. The Bushman brain presented to the College of Surgeons by Professor MARSHALL (D. 708) is not this brain.—G.E.S.

MARSHALL's table of measurements, in which he contrasts the European brain with the Bushwoman's, the European brain is smaller in certain dimensions. This indicates that he specially selected an abnormally small European brain for comparison.

Whilst the question of racial difference is one of great interest, it is necessary to emphasize that this is the description of the brain of an individual Bushwoman and therefore of morphological rather than of racial importance. It may be that the very primitive features to be described point to the lowly condition of the race to which she belonged; but in the present state of our knowledge the evidence of this from one specimen must be inconclusive. When working on the brain of the Australian aboriginal in Sydney, I found in twenty-five hemispheres that the sulcus lunatus was not a constant feature, and mentioned this fact to Professor ELLIOT SMITH (see MOTT Memorial Volume). In the following year I had the opportunity of examining another eight hemispheres in Brisbane and found in every one of them a well-marked sulcus lunatus. It must be emphasized, therefore, that whilst percentage occurrence of features may be of great importance, in a limited series they are not necessarily significant.

Concerning the remainder of MARSHALL's description it can be said that, apart from the sulcal pattern in which there are some errors in his figures, the information concerning the general form, relations, dimensions, and most of the sulci can be used with confidence. He was careful when removing the brain, already fixed *in situ*, to ascertain the extent of the deformation consequent upon fixation. Furthermore, his detailed description of the closure of the cranial sutures, of the form of the skull, and other observations permit the direct comparison of this interesting brain with the endocranial casts of fossil men and with the actual brains of modern races.

Of great importance in this brain are those areas on which so much stress has been laid by ELLIOT SMITH in primitive Man and by HENRY HEAD from the different standpoint of cerebral injuries in modern man. MARSHALL's own description of the general form, dimensions and relative position of the parts of the encephalon (pp. 508 and 509) is so accurate and complete that there is no need to enter into detailed discussion here on the matters already dealt with by him.

The General Form of the Brain.

The brain has suffered a certain amount of shrinkage (see fig. 25, Plate 3), which caused some flattening, but otherwise does not seem to have affected the shape.

The photograph of the ventral surface of the brain, fig. 1, Plate 1, shows the anterior perforated spaces, the optic tracts and the crura cerebri exposed to an unusual extent. The row of openings for the basal arteries, lying immediately posterior to the lateral olfactory tract, is plainly seen; and almost the whole of the orbital surface of the frontal lobe is exposed to view. The explanation of these facts is seen in the slender pointed appearance of the temporal poles. The temporal lobes are ill-developed so that they fail to extend forward and overlap the orbital surface. The orbital surfaces look narrow and their contour is sharply delimited from the temporal contour by a definite angle. The narrowness of the temporal lobe, seen both inferiorly and laterally, and its failure to extend in a forward direction are features which find their almost exact counterpart in the endocranial cast of *Homo rhodesiensis*, and in the brains of the aboriginal Australian. In one hundred Chinese hemispheres, which I have carefully surveyed and use as a standard group, there is not one hemisphere which is comparable in this regard with those of the Bushwoman. In all, the greater part of the anterior perforated space and a part of the sulcus orbitalis are hidden by the temporal pole. Of twenty-three Australian hemispheres thirteen show an extent of exposure comparable with that of the Bushwoman; but in these brains there is some deformity due to handling and defective fixation. Fig. 2 shows superimposed on the outline of the brain of the Bushwoman—taken from fig. 1, Plate 1—line drawings of the endocranial casts of the Rhodesian man, an aboriginal Australian, and a European. The diagram illustrates quite clearly the small size of the orbital surface of the frontal lobe and the narrowness of the temporal lobe of the brain of the Bushwoman. The other features of the orbital surface, the rostral keel, the hollowing of the surface and the form of the antero-lateral and postero-lateral angles of the orbital surface have been amply described by MARSHALL. When viewed from above, the brain affords a striking picture fig. 3, Plate 1. MARSHALL's description of this aspect of the brain is adequate, but it is necessary to draw attention to the position of the greatest expansion of the parietal lobe and to the peculiar form of the frontal lobe when seen from this aspect. In fig. 4 the same endocranial casts as used in fig. 2, and, in addition, that of *Pithecanthropus erectus*, are superimposed upon the hypothetical endocranial cast of the Bushwoman's skull. The form of the endocranial cast of *Pithecanthropus* and the Bushwoman, when viewed from this aspect, are very similar. The frontal lobe is slightly fuller and the occipital poles project more in the Bushwoman, otherwise the contours practically coincide.

As to the lateral aspect of the brain, MARSHALL's description gives all the salient features. This view when compared with the endocranial casts provides just as striking a picture as the views of the dorsal and ventral aspects, fig. 5. The endocranial cast of the Bushwoman, seen from the lateral aspect, is higher than that of *Pithecanthropus*; it is somewhat smaller than the endocranial cast of *Homo rhodesiensis* and differs from it in certain critical places. In *Homo rhodesiensis* the occipital region is somewhat longer and more square, the parietal region is somewhat flatter and the frontal region is more rounded and full.

In the temporal region the lower border of the temporal lobe is concave, the middle temporal sulcus is represented by shallow disconnected sulci and the width of the inferior temporal region is much reduced.

In ELLIOT SMITH's "Essays on the Evolution of Man" (1927) the significance of all these points (brought out by the examination of the general form of the brain and by a comparison of the contours of the different views with casts of fossil skulls) is quite apparent. It would appear from this examination of form that the Bushwoman's brain shows a degree of primitiveness and lowliness, which places it only slightly, if at all, above that of *Homo rhodesiensis.* This conclusion is verified by the form of

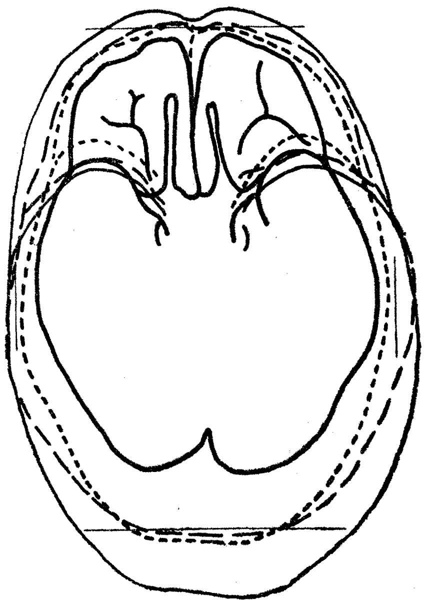

FIG. 2.—Outline of fig. 1, Plate 1, superimposed on the endocranial outlines of *Homo rhodesiensis,* an aboriginal Australian and a European. (Bushwoman, continuous thick line, *Homo rhodesiensis,* broken line with long strokes, aboriginal Australian, broken line with short strokes, European, continuous thin line.) The ruled lines indicate the maximum length and breadth of the Bushwoman from MARSHALL's measurements.

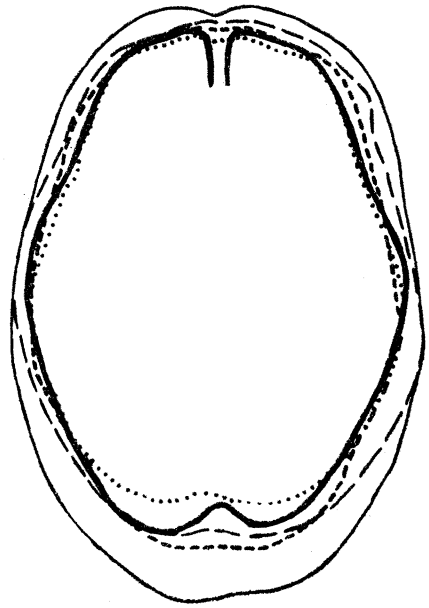

FIG. 4.—The hypothetical endocranial cast, reconstructed from MARSHALL's measurements, superimposed on the contours of the endocranial casts used in fig. 2, and in addition that of *Pithecanthropus* (dotted line).

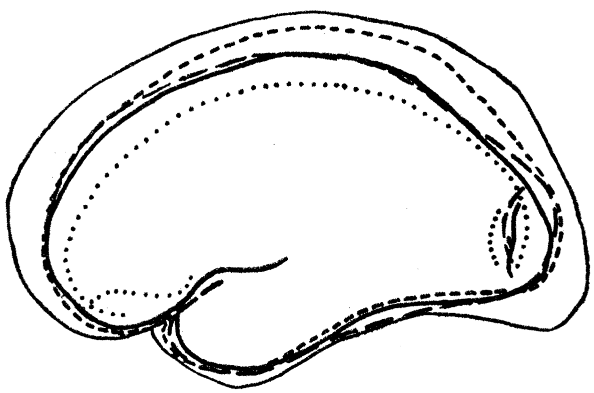

FIG. 5.—The same endocranial casts as used in fig. 4 seen from the lateral aspect.

the sulcal pattern. ARIËNS KAPPERS (1929), using cerebral indices, cites figures in his table on p. 242 which appear to confirm these conclusions.

It is necessary to discuss whether the small size of this brain may be merely an abnormal condition such as is sometimes found in the European, quite apart from maldevelopment; or whether the contracted frontal region may not be due to senile changes and therefore secondary. The first question cannot be adequately answered because the number of brains described has not been sufficient to warrant any conclusion. But we have the brain of the Hottentot Venus described by GRATIOLET (1854). GRATIOLET's fig. 2, Plate 11, shows the same features of form which have been described above. The wide appearance of the parietal region, narrowing rapidly forward to form an angle with the frontal contour, the square-cut appearance of the frontal lobes with the prominent antero-lateral angles and the simplicity of pattern of the sulci all reproduce the conditions so ably described by MARSHALL.*

Concerning the brain of the Hottentot Venus GRATIOLET says:

> "Cette femme . . . n'était point idiote. On peut remarquer, neanmoins, que les plis de son cerveau sont relativement tres-peu compliqués. Mais, ce qui frappe surtout, c'est la simplicité, l'arrangement regulier des deux plis qui composent l'etage supérior du lobe frontal. . . . Il y a, sous ce rapport, entre un cerveau blanc et ce cerveau de Femme bojesmane, une différence telle, qu'il est impossible de la meconnaître; et, si elle est constante, comme tout le fait supposer, elle constitue un des faits les plus intéressantes qui aient encore été signalée."

The question whether the small size of the frontal lobe is secondary is one of great interest in the light of the work by HARRIS (1928) on the changes in the skull consequent upon age. He has shown that the order of closure of the cranial sutures differs in the various apes, and that in Man the squamous suture remains open to old age. He has suggested that the order and time of closure of the sutures may have some definite relation to the different degrees of cerebral development. Fortunately, MARSHALL has given a very exact account of the sutures in the skull and their state indicates that the Bushwoman was aged. A Bushman's skull in the Amsterdam collection presents closure of all the sutures except the squamous. This skull was definitely aged and the inner table was flattened and thickened under the frontal eminence. HARRIS has shown that this thickening of the frontal bone takes place mainly in the inner table as a senile age change. MARSHALL records that the average thickness of the frontal bone was 0·35 of an inch, increasing at the forehead itself to 0·5 of an inch.

* Since this account was written a paper by ISIDORE SLOME (1932) on the Bushman brain has been published. Five hemispheres are described and the following statements may be quoted: "*Narrow width of frontal lobes* (*or rather pronounced parietal width*). This feature which is conspicuous in both MARSHALL's and KOCH's (1867) Bushwomen's brains (KAPPERS, 1929) is also well shown in the present collection, particularly in brain 3. This is in keeping with the characteristic shape of the Bushman cranium."

"The weights of the three brains are (i) 965 gm., (ii) (half) 425 gm., and (iii) 1097 gm."

"Indubitably, therefore, the weight of the Bushman brain is lower than that of any other living race of Man as yet recorded."

The weight of the brain examined by MARSHALL is given by him as probably not more than 872 gm.

Despite these facts it seems improbable that this increase of thickness of the inner table of the skull would make an appreciable difference to the form of the frontal lobe; and, making full allowance for cerebral shrinking incidental to old age, the form of the brain should not be much affected. It is, however, a question worth investigating.

It is important that the age of suture union should be determined in primitive races in order to ascertain whether there is a definite precocity of closure in association with a definite and early final attainment of growth in the brain.

The Sulcal Pattern of the Brain.

The occipital region.—Fig. 6, Plate 2, is the photograph of the posterior aspect of the brain. This photograph, perhaps the most interesting of the series, was not published by MARSHALL. Fig. 7 is a line drawing reconstructed from this and the

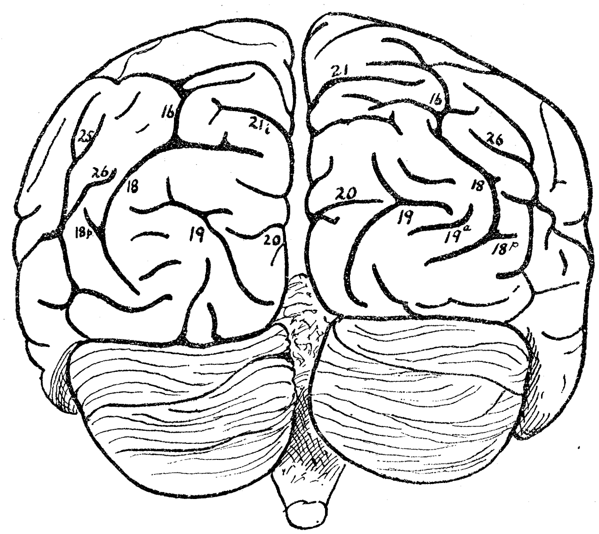

FIG. 7.—Reconstructed line drawing of fig. 6, Plate 2.

other photographs. A careful comparison of the different views makes it possible to form an idea of the amount of submergence or separation of the sulci. Viewed from behind the occipital or lunate operculum (18) is prominent on both sides. On the left side the lunate sulcus extends from a point about one centimetre from the lateral border of the hemisphere to a point close to the medial border. Antero-superiorly the operculum appears to cover completely the sulcus occipitalis transversus (17) and, medial to the sulcus paroccipitalis, forms the posterior boundary of the arcus parieto-occipitalis. Near its medial termination a short branch of the lunate sulcus passes forward into the arcus parieto-occipitalis; this is probably the inner end of the buried sulcus occipitalis transversus. In front of this is a sulcus passing from the medial surface into the arcus parieto-occipitalis. This is the incisura parieto-occipitalis (21*i*) which ends in the arcus intercuneatus on the medial surface. On the right side the occipital operculum is almost as extensive as on the left side. Antero-superiorly, however, the relations are somewhat different; here the operculum involves the outer limb of the sulcus occipitalis transversus, the medial limb being free. Immediately posterior to the medial limb of the sulcus occipitalis transversus there is a curved sulcus cutting the dorso-medial border of the hemisphere. I regard this as the sulcus polaris superior of BOLTON (1914); but, as there is no record of the medial surface of the right hemisphere, its exact identity cannot be determined with certainty. On both sides a short sulcus prælunatus (18*p*) arises from the convexity of the lunate (opercular) sulcus and is normally disposed. The form of the intrastriate sulci—external calcarine (19) and accessory external calcarine (19*a*)—makes it practically certain that the area striata almost completely covered the occipital poles and extended almost as far as, if not actually to, the posterior lip of the occipital operculum. On the right side the Y-shaped form of the sulcus calcarinus externus is very ape-like. I have found it in this form in twenty per cent. of the Australian hemispheres and in three per cent. of the Chinese hemispheres. In one Australian hemisphere on the right side I have seen an operculation very similar in form to that seen on the right side of this brain, and in it the form of the lateral intrastriate sulci is almost exactly the same. Also in the Australian brain (No. 5 of the Sydney collection), described by FLASHMAN (1908), the left side is almost exactly identical in appearance with the left side of the Bushwoman's brain even to the form of the sulcus calcarinus externus. I have never seen a brain in which there is such an extensive area of striate cortex on the lateral aspect of the hemisphere on both sides; although in thirty-six hemispheres of aboriginal Australians I have seen two hemispheres, both right side, which appear to be more extensive than either of these; in one it is equal in size. The Australian described by KARPLUS (1902) had an operculation which appears to be as great. And finally, in the examination of many hundreds of Chinese brains, although I have come across many extensive opercula, none was equal to these shown in this Bushwoman.

Anterior to both lunate sulci there is on each side the sulcus occipitalis anterior (26) forming a completely curved arcade lying parallel with the lunate (opercular) sulcus. This condition occurs very commonly in the Australian brain—as it does also in the brains of the higher anthropoids—and it strongly suggests that the same factors determine the form both of the lunate sulcus and of the sulcus occipitalis anterior. In higher types the breaking down of the lunate operculum is accompanied by a breaking down of the anterior occipital sulcus and leads to a greater complexity of the pattern of the sulci in the parietal lobe. This will be further considered in dealing with the parallel sulcus. As the elucidation of the morphology of the occipital region is a recent achievement it is not surprising that MARSHALL failed to recognize the lunate operculum on both sides. He attempted to bring the pattern of the sulci into conformity with GRATIOLET's division of the occipital lobe into lateral occipital gyri and sulci; and, further, homologized, as far as one can see, the sulcus occipitalis anterior with the external perpendicular sulcus of older writers and homologized this with the external perpendicular sulcus of the apes.

The absence of an exact knowledge of the occipital region at the time is evident from MARSHALL's failure to reproduce what was perhaps his most interesting photograph, and in passing over the lithographic error in his Plate 18, fig. 3, where the upper end of the sulcus occipitalis anterior is shown as being confluent with the intraparietal system, instead of being free as the photographs of the posterior and lateral aspects clearly show.

Thus the lunate opercula are extensive and fully curved and involve the sulci occipitales transversi; the form of the lateral intrastriate sulci is primitive; the sulci prælunati are short and typically placed; and finally, the sulci occipitales anteriores form complete arcades lying concentrically with the lunate opercular sulci.

The Sulcal Pattern of the Lateral Surface.

Figs. 8 and 9 show the sulci on the lateral surfaces of the brain of the Bushwoman, and fig. 10, taken from ELLIOT SMITH's "Studies in Morphology" (1904, fig. 25) the

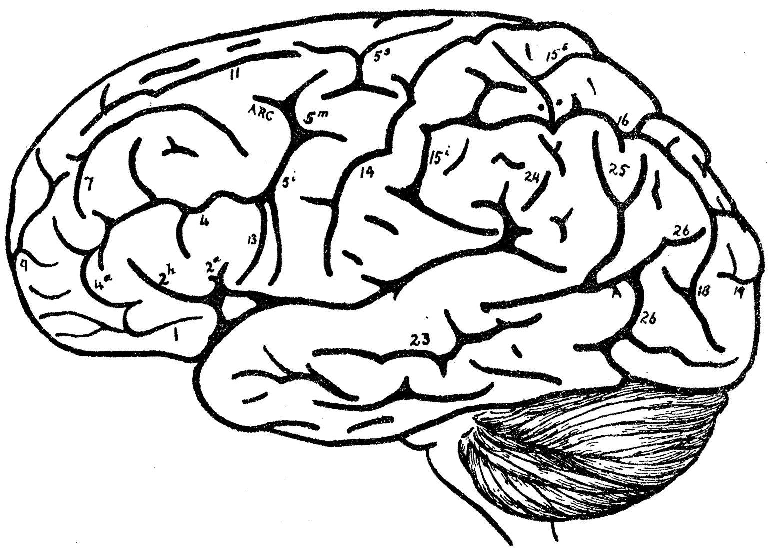

FIG. 8.—Line drawing of the lateral aspect of the left hemisphere shown in Fig. 11, Plate 2.

lateral surface of the brain of a Negress, which he describes as "exhibiting a greater assemblage of primitive features than probably any other human brain ever recorded."

These three figures of the two hemispheres in the Bushwoman and the one hemisphere of the Negress furnish a standard type of primitive features for the purpose of assessing variation in pattern and development of the numerous Chinese and Australian brains which I have examined.

The insular region.—The anterior part of the cortex of the island of Reil is visible from the surface on both sides. In many of the Australian brains the insula is exposed to a similar degree; but, whereas in them the hemispheres are considerably distorted, the accurate account given by MARSHALL makes it certain that the condition is normal to the brain of this Bushwoman. In this brain the position and form of the temporal pole is of significance.

The encroachment of the temporal lobe on to the under surface of the frontal lobe merits attention. The evolutionary growth of the brain has necessarily proceeded

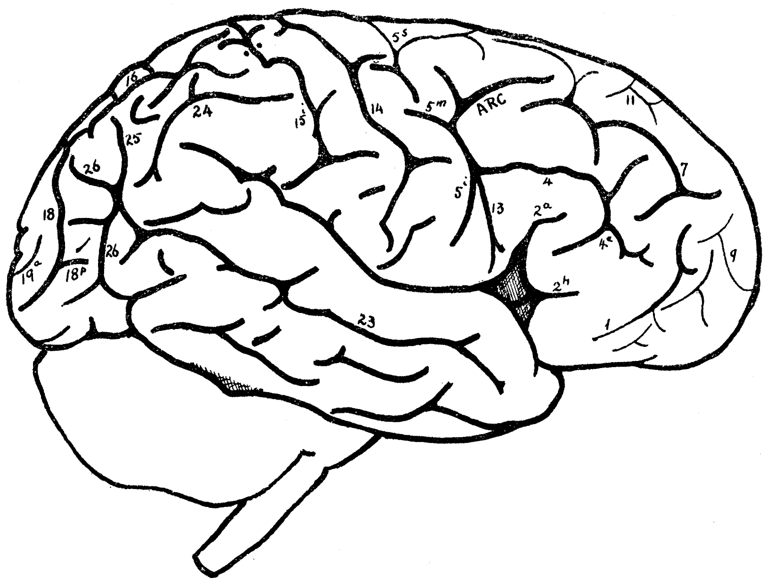

Fig. 9.—Line drawing of the lateral aspect of the right hemisphere shown in fig. 12, Plate 2.

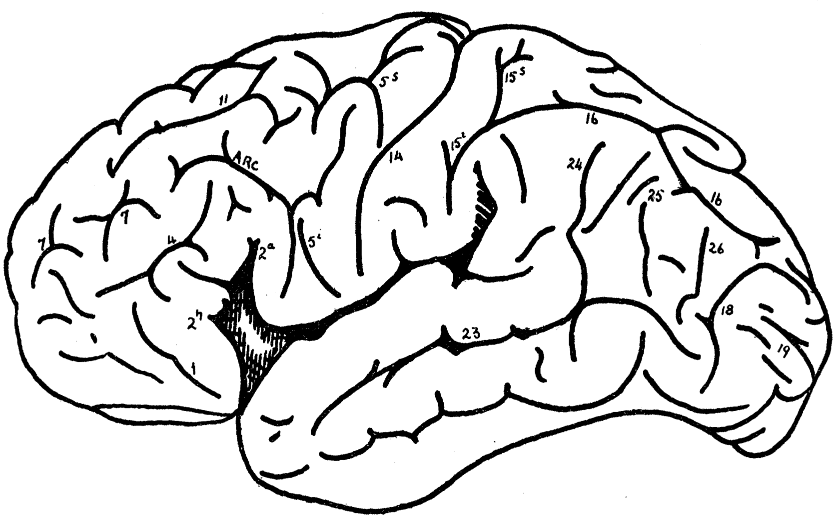

Fig. 10.—The lateral aspect of the left hemisphere of the brain of a Negress (taken from Elliot Smith's "Studies in Morphology," fig. 25).

pari passu with a series of changes in the growth of the cranial cavity itself. In these parallel growth changes brain areas do not necessarily correspond with skull areas either phylogenetically or ontogenetically. For example, the edge of the lunate operculum lies anterior to the lambdoidal suture in the Chimpanzee, coincident with it in many Australian hemispheres, and posterior to it in the Chinese. Again, in the fœtus at the fifth month, the sulcus præcentralis inferior lies anterior to the coronal suture, at the eighth month it lies behind it, and at birth the forward movement of the sutural line becomes more marked (CUNNINGHAM (1892), p. 301). KEITH (1931) makes use of the term "frontal cap of Anthony" in describing the endocranial cast of the Galilee skull. This cap must not be confused with the frontal cap of Broca which is used clinically for a definite region in the human brain and which may, or may not, correspond with the frontal cap of Anthony. The so-called frontal cap of Anthony is very similar in appearance and apparently in position, in brains ranging from Cercopithecus to Man. This frontal cap is not necessarily homologous in the different forms. In the Cercopithecidæ it is formed of cortex which constitutes the lower part of area 6 of BRODMANN (1909; fig. 90). The lower end of the sulcus arcuatus is a sulcus within area 6 at this point and it, together with the maximum convexity of the frontal cap, lies actually anterior to the tip of the temporal pole. In Man (BRODMANN, 1909 (fig. 85)) this region—the lower end of the sulcus præcentralis inferior within area 6—lies well posterior to the ascending limb of the fissure of Sylvius and also to the tip of the temporal pole. There is, however, a frontal cap in Anthony's sense. This lies anterior to and below the anterior horizontal limb of the fissure of Sylvius and is actually overlapped by the temporal pole. The cortex of this cap consists of areas 45 and 47 of BRODMANN. The anterior end of the temporal pole lies well under the frontal lobe. Careful study of the sulcal pattern in the anthropoids shows all the intermediate stages in the forward encroachment of the temporal pole. In this process, as evolution proceeds, the upper border of the temporal lobe covers in turn the cortex related to the lower end of the sulcus arcuatus, the expanding frontal region developing around the region of the upper end of the sulcus fronto-orbitalis and related to areas 6 and 8 of BRODMANN, and finally, the cortex lying anterior to this, in the undersurface of the frontal lobe. The arrangement of the arteries, which I have described elsewhere (1930) clearly shows these changes. I am therfore in agreement with KEITH (1931, p. 79) that it is the lateral region of the frontal lobe which expands, and not the orbital. I also agree that the sulcus rectus at the frontal pole becomes homologous with the medial part of the sulcus fronto-marginalis and probably with the anterior part of the sulcus frontalis medius. A part of the brain so variable in its nature as the frontal cap cannot be used for the purposes of homologizing the sulcus fronto-orbitalis with the sulcus subfrontalis. I hold to the original opinion of CUNNINGHAM that the homologue of the sulcus fronto-orbitalis in Man is the anterior limiting sulcus of the island of Reil. I differ from CUNNINGHAM, however, in also regarding the anterior horizontal limb of the fissure of Sylvius as the homologue of the upper end of the sulcus fronto-orbitalis of the apes. A very striking picture of the change taking place at the anterior part of the island of Reil is seen in the figures of the brains of a mother and child described by KARPLUS (1905).

In the brain of the Bushwoman, the temporal pole exhibits a condition intermediate between that in the Anthropoid apes and that in higher races where the insula is completely hidden. The features of the condition as seen in the Bushwoman are :—

(1) The exposure of the orbital surface of the frontal lobe—already referred to.

(2) The slender temporal pole reaching little beyond the level of the point of junction of the two anterior limbs of the fissure of Sylvius.

(3) The position of the lower end of the sulcus præcentralis inferior (5*i*) (a sulcus within area 6 of BRODMANN) only a short distance posterior to the level of the temporal pole.

(4) The curious shelf-like form of the anterior third of the main horizontal limb of the fissure of Sylvius referred to by MARSHALL.

All these features prove conclusively that the exposure of the island of Reil is directly due to a failure in development of the temporal lobe and a corresponding lack of development of the frontal lobe.

The horizontal shelf-like form of the anterior part of the fissure of Sylvius is produced by the bulging of the cortex surrounding the lower ends of the sulci centralis (14) and præcentralis inferior. This convex bulging indents the upper border of the temporal lobe, and, using the sulci and areas 4 and 6 of BRODMANN as criteria for homology, it corresponds with the area in the Cercopithecidæ which has been termed the frontal cap. Comparing fig. 90 of BRODMANN, fig. 13 of this paper, showing the lateral surface

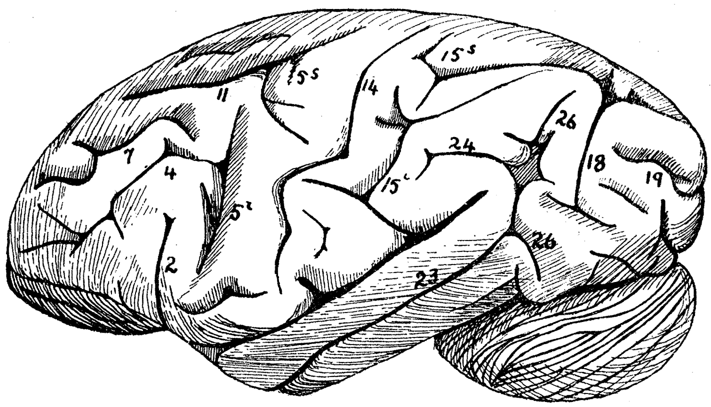

FIG. 13.—The lateral view of the left hemisphere of the brain of a Gorilla in the Institute of Anatomy, University College, London.

of the brain of a Gorilla, with fig. 8, showing the right lateral surface of the brain of the Bushwoman, it is at once clear that areas 4 and 6 have taken up a different position relative to the temporal pole as the frontal lobe has expanded. In the Cercopithecidæ the tip of the temporal pole lies at the level of the line of contact of areas 4 and 6 (BRODMANN, fig. 90); in the Gorilla's brain, fig. 13, the relations are approximately the same on the left side, and in the Bushwoman the temporal pole has shifted forward so that areas 4 and 6 lie posterior to the temporal pole. In the brain of the European, using BRODMANN's fig. 85, the lower part of the frontal lobe is still further encroached upon by the temporal lobe. The observations of CUNNINGHAM on the changing relations between the coronal suture and the sulcus præcentralis inferior in ontogeny are exactly paralleled in the phylogenetic changes; and the dynamic centre of growth in the frontal lobe is proved to be on the lateral surface of the frontal lobe lying anterior to areas 6 and 8, causing the backward displacement of area 6 and the upward displacements of areas 8 and 9.

The Parallel Sulcus and its Terminal Branches.

On account of the confusion concerning the correct definition of the sulcus temporalis superior, the term parallel sulcus is used in this paper; and by its terminal branches are meant the various sulci in the inferior parietal lobule with which it may become connected. It must not be inferred, however, that these sulci are necessarily derived morphologically from the parallel sulcus.

The pattern of the sulci of the parietal region of the brain of the Bushwoman appears to represent a critical stage for the understanding of the evolution of this area. For this reason, it is desirable to refer briefly to the evolutionary changes which appear to have brought about the expansion of the parietal lobe. The difficulties of establishing exact homologies in terms of cortical pattern are apparent from the writings of JEFFERSON (1913), INGALLS (1914) and others. Whilst the works of these two authors have been freely consulted, it is not intended to discuss them here.

In the Cercopithecidæ (see BRODMANN, fig. 90) the so-called sulcus intraparietalis, so far as it appears on the surface, has cortical relations which are those of the sulcus postcentralis in Man; the parallel sulcus in its upper part separates areas 19 and 7, and in its lower part areas 21 and 22; and the posterior part of the fissure of Sylvius lies between areas 22 and 7. The only sulcus in Man to retain any of these cortical relations is the part of the parallel sulcus lying between areas 21 and 22. The greater part of the new areas, arising first in the higher anthropoids and reaching their full development in Man, are interposed between areas 22 and 7 inferiorly and between areas 19 and 7 superiorly. Therefore, using cortical areas as criteria for homology of the sulci, either all the sulci between these areas in Man must be homologous with the posterior end of the fissure of Sylvius and the upper end of the parallel sulcus of the Cercopithecoidea, or, as I believe, they should be regarded as new sulci in the course of evolution in the higher anthropoids and Man. Similarly, the major part of the sulcus intraparietalis is newly evolved.

I have discussed elsewhere (1927) the separate nature of the sulcus temporalis anterior and of that part of the parallel sulcus which separates areas 21 and 22—the inferior parallel sulcus. In the same paper the development of the sulcus occipitalis from the superior parallel sulcus was discussed.* Those views on the changes taking

* I should here like to take the opportunity of withdrawing a statement, which I now believe to be wrong, made in that paper that the posterior end of the fissure of Sylvius can be used as a fixed point for cerebral survey.

place in the centre of the parietal lobe can be amplified here before proceeding to the description of the Bushwoman. I am enabled to place on record the sulcal pattern of a Gorilla through the courtesy of Professor ELLIOT SMITH. Figs. 14 and 15 show the lateral aspects of this brain.

It is evident that a dynamic point in the parietal lobe lies at the point of junction of the branches (24, 26) of the parallel sulcus towards which the sulcus prælunatus points. The pattern of the sulci has the form of an X. The two posterior limbs of the X constitute the sulcus occipitalis anterior (26) whose form is apparently determined by the

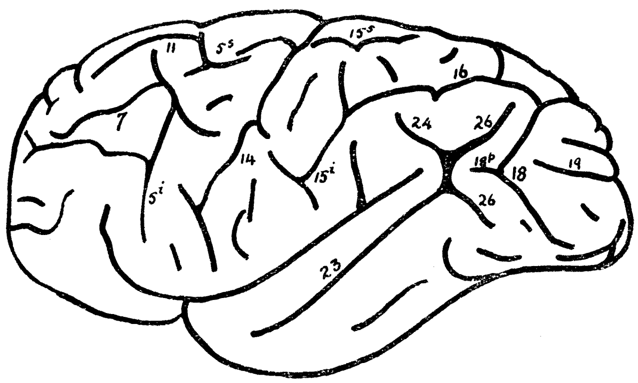

FIG. 14.—The left hemisphere of the brain of the Gorilla represented in fig. 13.

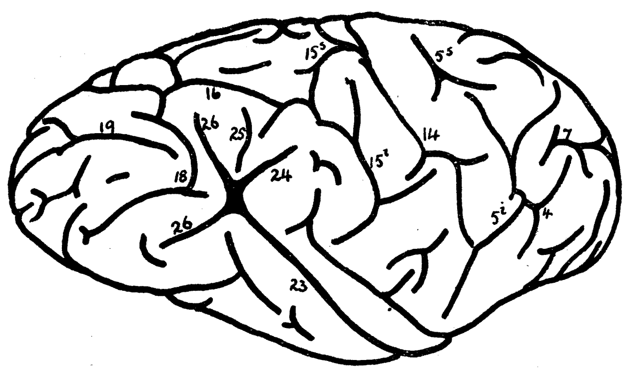

FIG. 15.—The right hemisphere of the same brain.

same factors as those determining that of the sulcus lunatus (18). The antero-superior arm of the X is the superior parallel sulcus (24). It turns round the posterior end of the fissure of Sylvius and is directed towards the concavity formed by the upper part of the sulcus postcentralis inferior (15*i*). It is definitely a sulcus (24) of the supramarginal lobule. The antero-inferior arm of the X meets the inferior parallel sulcus and is frequently separated from it either superficially or deeply. The further expansion of the part of the inferior parietal lobule placed between the two superior arms is indicated by a compensatory sulcus which may be definitely named the sulcus angularis (25). The earlier stage in the expansion of the dynamic centre in the parietal lobe is well shown in the brain of the Chimpanzee depicted by CUNNINGHAM (1892 ; fig. 48).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Here the two posterior limbs have not become completely extruded from the parallel sulcus at the convexity of its curve. In fig. 16, illustrating the lateral surface of the

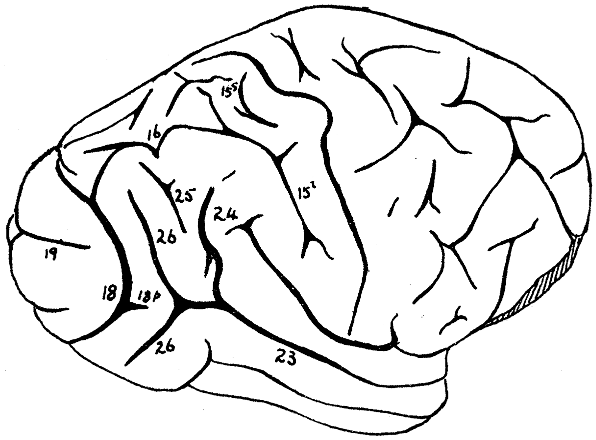

Fig. 16.—The lateral view of the right hemisphere of the brain of an Orang utan, showing the appearance of the sulci of the inferior parietal lobule.

brain of an Orang utan, the posterior extrustion of the sulcus occipitalis anterior (26) has progressed further so that it is now connected with the parallel sulcus (23) by a sulcus annectans. Frequently the sulcus annectans is broken by a superficial or deep gyrus and the sulcus occipitalis anterior appears as a separate sulcus. I am indebted to Dr. Ariëns Kappers for a photograph of the brain of an aboriginal Australian, fig. 17, Plate 3. A line drawing of the parietal area (fig. 18) shows the X-like appearance

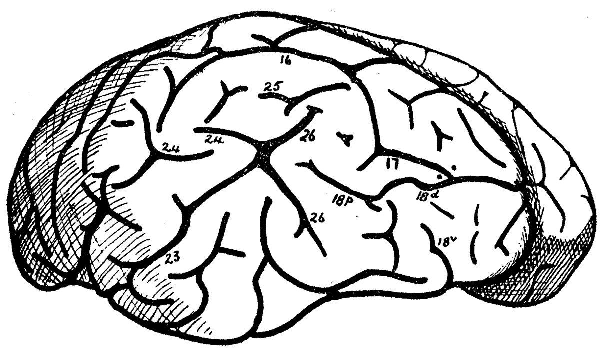

Fig. 18.—A line drawing of fig. 17, Plate 3.

of the branching of the sulci of the parietal lobe, the relative expansions of the supramarginal lobule and of the area præoccipitalis as compared with the anthropoid brains, and the separation of the superior parallel sulcus within the supramarginal lobule.

The interpretation of the sulci of the parietal region of the brain of the Bushwoman is now comparatively simple. On the left side the parallel system is divisible into three parts; anteriorly, the sulcus temporalis anterior lies in relation to the temporal pole and is separate from the inferior parallel sulcus; below and parallel with the fissure of Sylvius, the inferior parallel sulcus (23) is clearly defined and is separate from the sulcus temporalis anterior in front, and from the remainder of the parallel system posteriorly. At the site which can be assumed to be the posterior limit of areas 21 and 22 of Brodmann, the sulcus continuing the parallel system to the dynamic centre of the parietal lobe overlaps the inferior parallel sulcus and is separated from it by a superficial gyrus, fig. 8. The sulcus occipitalis anterior (26) has become separated from the bend of the parallel sulcus, but is still connected therewith by a sulcus annectans (A); it forms an arcade parallel with the lunate (opercular) sulcus, and it is confluent inferiorly with the sulcus occipitalis inferior and with the sulci of the præoccipital notch. This inferior confluence of sulci produces a more complicated picture than that seen in the higher anthropoids and is an expression of the expansion producing area 37 of Brodmann. The superior branches of the parallel system consist of (*a*) a group of separate and small sulci in the gyrus supramarginalis, representing the superior parallel sulcus (24), (*b*) a branched sulcus angularis connected with the sulcus annectans (25), and (*c*) the upper half of the sulcus occipitalis anterior (26). This arrangement is clearly comparable with the pattern seen in the Gorilla, Orang, and Australian brains depicted; and it seems justifiable to suggest the derivation of the Bushwoman pattern from some such types. Apart, however, from the primitive arrangement of these sulci there is definite evidence of lack of development and folding of the inferior parietal region as shown by the simple form of the arcade formed by the sulcus intraparietalis. It is quite unusual in the human brain to see a parietal lobe in which there are no fissural foldings passing into the inferior parietal lobule from the sulcus intraparietalis. Finally, attention is drawn to the peculiar form of the posterior end of the fissure of Sylvius. The curious anteflexed form of the ascending terminal limb is frequently seen in the brains of the anthropoids but seldom in the human brain.

On the right side, fig. 9, although the sulcus temporalis anterior and the posterior part of the parallel system are confluent with the inferior parallel sulcus, the pattern of the sulci is fundamentally the same. The superior parallel sulcus (24) is separated from the remainder of the parallel system. It arches over the posterior end of the fissure of Sylvius and its anterior end is directed towards the concavity of the sulcus postcentralis inferior (15*i*). Thus it exactly corresponds with the antero-superior arm of the X in the Gorilla's brain. The sulcus occipitalis anterior (26) forms a complete arcade lying parallel to the sulcus lunatus; inferiorly it is confluent with the sulcus of the præoccipital notch and with a detached element of the sulcus temporalis medius. The angular sulcus (25) is confluent with the upper part of the sulcus occipitalis anterior to form a Y-shaped sulcus which is continuous, through the sulcus annectans with the inferior parallel sulcus.

Comparison of the endocranial casts of *Homo rhodesiensis*, an Australian and a European with the brain of the Bushwoman suggests that the expansion of the inferior parietal lobule first takes place in the supramarginal lobule and extends backwards as evolution proceeds. The comparison of the arrangement of the superior parallel sulcus (24) in the anthropoids, Australian and Bushwoman also suggests this. In Rhodesian Man and in the Australian the region behind the supramarginal lobule is flattened as it is in the Bushwoman. In the Bushwoman the sulcal pattern and the form indicate the greater size of the supramarginal lobule and the relatively short distance from the parietal bulging to the occipital pole. The occipital operculum appears to be little disturbed by the parietal expansion and the præoccipital gyrus lying between the sulcus occipitalis anterior and the sulcus lunatus is distinctly narrow. In the European the parietal bulging is extensive and consequently the areas of the angular and postparietal lobules are larger. This is in keeping with the greater com-

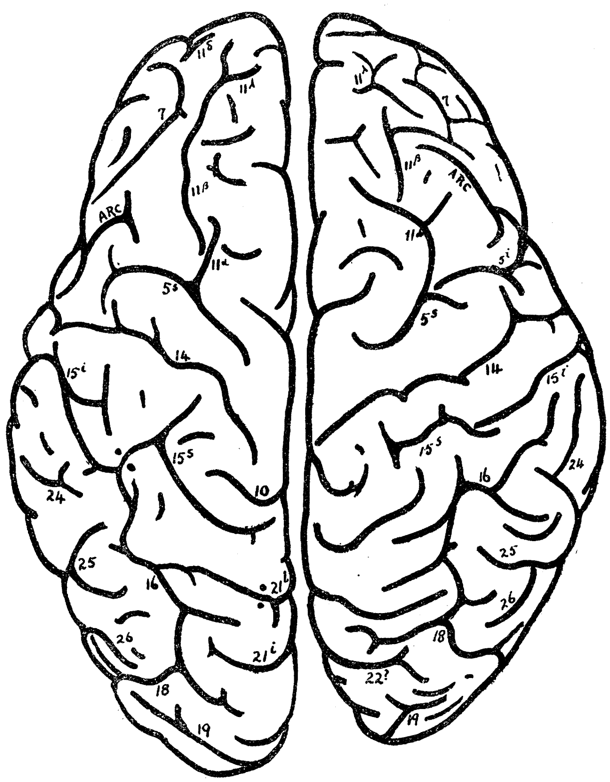

FIG. 19.—The sulcal pattern of the dorsal aspect of the brain of the Bushwoman.

plexity of the pattern of the sulci in the European, with the greater extent of the folding of the sulcus intraparietalis and with the breaking down of the lunate operculum, fig. 19 (compare 18 on the two sides),

Superior parietal lobule.—On the left side the sulcus centralis (14) falls short of the medial border, where it ends in a concavity formed by the upper end of the sulcus cinguli (10). Between the sulcus cinguli and the point at which the sulcus limitans præcunei (21*i*) cuts the dorsal border, to become superficially confluent with a branch of the sulcus intraparietalis, the long posterior arm of the sulcus postcentralis superior alone intervenes. The sulcus postcentralis superior (15*s*) consists of a short stem, which appears to be separated from the inferior postcentral sulcus by a slightly submerged gyrus, and two superior arms, a short anterior and a longer posterior. These two arms form an arcade around the upper end of the sulcus cinguli. In the Chimpanzee brain (SHELLSHEAR, 1930), the form of the sulcus postcentralis superior on both sides was similar to that on the left side of the Bushwoman. MINGAZZINI (1928) shows in many of his figures of Chimpanzee and Orang brains the same form; and I have frequently found it in Gorilla and Orang brains. From the comparison of the arterial supply to cortical areas in the Anthropoids and Man it would appear that the expansion of the cortex in the region of the upper end of the sulcus cinguli has brought about the separation of the posterior arm of the sulcus postcentralis, the separated sulcus being named in human anatomy the sulcus parietalis superior. BRODMANN'S figure, showing the relations of the cortical areas to the sulci in Man, is difficult to interpret; but from his description the anterior arm of the sulcus postcentralis superior would appear to separate areas 2 and 5, the sulcus cinguli 5 and 7, and the sulcus parietalis superior is a sulcus within area 7. ELLIOT SMITH (1907) shows a very similar relationship, but, in his figures, area 7 of BRODMANN is subdivided into areas parietales superiores A and B with the sulcus parietalis superior separating them from one another. The right hemisphere of the Bushwoman shows a separation of the posterior arm of the sulcus postcentralis superior; and the cortical relations depicted by ELLIOT SMITH can be assumed from the sulcal pattern.

The Præcuneus.—The præcuneus on the left side is bounded posteriorly by a sulcus which branches close to the medial border of the hemisphere. Whilst the meaning of the arrangement of the sulci of the fossa parieto-occipitalis will be dealt with when the medial surface of the occipital region is considered, it will suffice here to state that the main stem of the branched sulcus together with the small posterior branch is considered to be the sulcus limitans præcunei (21*l*). The sulcus which appears to continue the sulcus limitans præcunei over the dorsal border is regarded as part of the intraparietal system and is only superficially confluent with the sulcus limitans præcunei. Within the præcuneus there lies a branched sulcus; the upper vertical arm is the sulcus præcunei, the lower horizontal arm is the sulcus subparietalis (30). The sulcus præcunei is a sulcus separating the superior parietal areas A and B of ELLIOT SMITH and the sulcus subparietalis bounds the area parasplenialis. Fig. 20 (Plate 3), and figs. 21 and 22 show respectively the photograph, the line drawing, and the hypothetical areas of the medial surface of the brain of the Bushwoman. In the Australian I have found that the sulcus limitans præcunei is vertically disposed, that the upper part of the præcunei is ill-developed and that there is a failure of development of the operculum anterior fossæ parieto-occipitalis. The same features are found in this hemisphere of the Bushwoman. The narrowness of the præcuneus between the upper curve of the sulcus cinguli and the upper end of the fissura parieto-occipitalis is appreciated by comparing this hemisphere with all the figures of the medial surface depicted in RETZIUS'S "Das Menschenhirn" or, as I have been able to do, with orthogonal drawings of one hundred Chinese hemispheres. In this way the form of the præcuneus definitely shows that the upper part of the superior parietal lobule is ill-developed. The large lunate opercula, the simple pattern of the inferior and superior parietal lobules, and the simple form of the sulcus intraparietalis all point to a failure in development of the territories bounding the visuo-sensory and visuo-auditory bands of ELLIOT SMITH. We are thus justified in assuming that the parietal and occipital regions indicate that

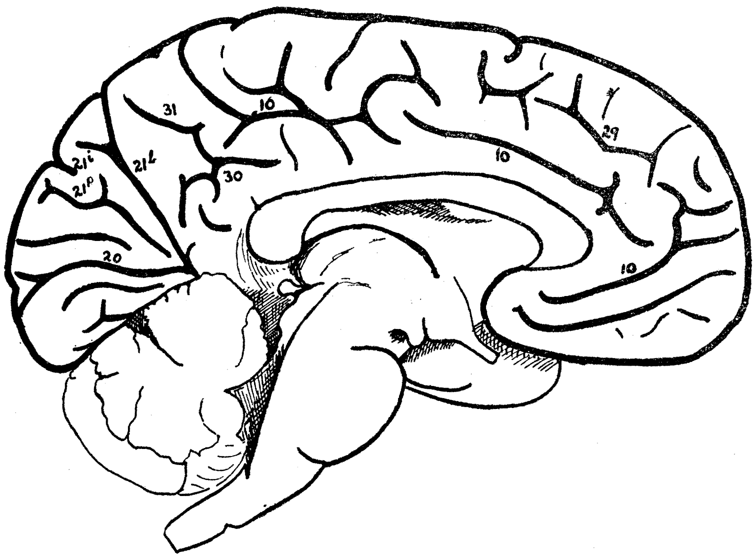

FIG. 21.—Line drawing of fig. 20, Plate 3.

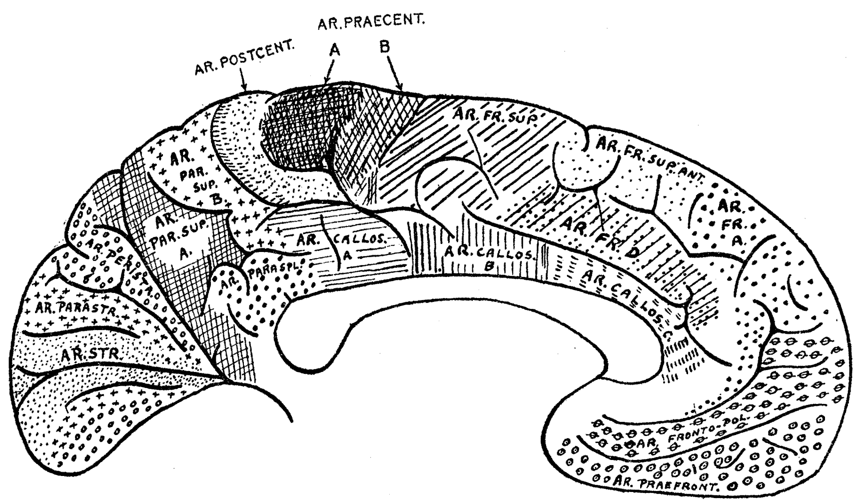

FIG. 22.—Hypothetical reconstruction of the cortical areas of the left hemisphere (after ELLIOT SMITH).

this Bushwoman's brain is intermediate in development between an advanced Gorilla-like type and a highly evolved human brain.

The Intraparietal Sulcus.—The main features of this sulcus have already been described and its form is well shown in the various figures. The only feature which needs special comment is the well-marked sulcus postcentralis transversus of EBERSTALLER. It lies obliquely across the lower end of the inferior postcentral gyrus and is confluent with the sulcus postcentralis inferior.

The Frontal Lobe.

The exact description of the sulci of the frontal lobe cannot be satisfactorily carried out until the vexed problem of their homologies has been settled. Three clearly defined sulci—the arcuate, rectus and fronto-orbitalis—exist in lower forms. The evolutionary changes producing the extensive new areas in Man cause such displacements and changes of form that it is difficult to trace them.

BRODMANN's figures show that the anterior part of the sulcus frontalis medius and the sulcus fronto-marginalis are the only sulci which can represent the sulcus rectus, if cortical pattern is to be used as a criterion, for these two sulci are both related to area 10. Moreover, the relations of the arteries to the sulcus rectus in the apes are the same as the relations of the same arteries to the anterior part of the sulcus frontalis medius and the sulcus fronto-marginalis in Man. It appears that the sulcus fronto-orbitalis of the apes is represented either wholly or in part by the orbital opercular sulcus of the island of Reil, and that the sulcus arcuatus is represented in its lower part by the sulcus præcentralis inferior and in its upper part by sulci which may be found to lie between areas 6 and 8 of BRODMANN. Such sulci may sometimes be found to agree with a part of the sulcus frontalis medius system, or even with a part of what would be named sulcus frontalis superior so variable is the pattern of the sulci and the levels at which the diagrammatically conceived sulci are found.

The Sulcus Frontalis Superior (11).—(Figs. 3, 8, 9, and 19). Posteriorly this sulcus forms an integral part of the sulcus præcentralis superior (5*s*). In the anthropoids a continuous sulcus frontalis superior is rare. The sulcus præcentralis superior is a triradiate sulcus with one arm directed anteriorly and the other two lying parallel with the sulcus centralis and limiting the upper part of the precentral area. I have named the anterior arm the element "α" of the sulcus frontalis superior (11α). On both sides of the brain of the Bushwoman the triradiate form is typical although somewhat more complex on the right side. In the Chimpanzee I have shown the arterial relations to the remainder of the sulcus frontalis superior and named the parts of it "β," "γ," and "δ," regarding the element "δ" as an anterior branch which frequently fuses with the sulcus fronto-marginalis of WERNICKE. These elements of the sulcus frontalis superior nearly always lie obliquely on the hemisphere with their anterior ends directed towards the medial border. On the left side "β" and "γ" are confluent with one another and constitute a separate sulcus whose anterior end is directed medially, and "δ" is confluent with the sulcus fronto-marginalis. Between the sulcus frontalis superior and the medial border of the hemisphere there are detached sulci representing the sulcus frontalis medialis. On the right side "β" appears to join the sulcus frontalis medius (7), but this is not certain on account of fading of the photographs in this region; "γ" is a separate branched sulcus having the form of an H and "δ" is confluent with the anterior end of the sulcus frontalis medius.

The Suclus Frontalis Medius (7).—On the left side this sulcus forms a curve convex upwards. It extends from the region of the angle formed by the sulcus præcentralis inferior and the sulcus frontalis inferior to a point in close proximity to the element "δ" of the sulcus frontalis superior. On the right side the sulcus frontalis medius occupies the same position as on the left side. It is somewhat more complicated, however, in its branching on account of secondary connections with parts of the sulcus frontalis superior.

The Sulcus Frontalis Inferior (4).—On both sides this sulcus is well defined, forming an arcade over the frontal operculum or pars triangularis. The form of the sulcus and its relations with the anterior part of the fissure of Sylvius are, however, somewhat different on the two sides and so each will be described separately. On the left side it arises from the lower third of the sulcus præcentralis inferior (5*i*) at the point where this sulcus appears to divide into two branches. Unfortunately at this point the presence of submerged gyri cannot be determined; but it seems certain that the anterior of the two branches is the sulcus diagonalis (13), and the posterior the lower end of the sulcus præcentralis inferior (5*i*). Superficially the sulcus frontalis inferior takes a wide sweep to form an almost complete circle around the two anterior limbs of the fissure of Sylvius. It appears from the photograph that the anterior part, where it turns back under the anterior horizontal limb of the fissure of Sylvius, is separated from the main sulcus frontalis inferior by a slightly submerged gyrus; and that the anterior part is constituted by a sulcus radiatus joined with the sulcus subfrontalis. The sulcus frontalis inferior proper forms two arcades directed inferiorly. The posterior arcade arches over the ascending limb of the fissure of Sylvius; the anterior over the horizontal limb. The branch of the sulcus frontalis inferior separating the arcades is an axial sulcus within the pars triangularis. Superiorly two short branches pass into the gyrus frontalis medius.

At first sight the condition of the sulcus frontalis inferior on the right side appears to be similar to that on the left side, but the difference in form and position of the pars triangularis makes this improbable. On the left side the base of the pars triangularis is directed upwards, whereas on the right side it is directed forwards. This difference in form causes the arcade over the ascending limb on the right side to be more extensive than on the left side; and, if the pars triangularis on each side is homologous, the axial furrow of the right side would correspond with the furrow separating the two arcades on the left side, thus indicating a greater development of the cortex surrounding the ascending limb of the fissure of Sylvius on the right side. The sulcus subfrontalis (1) on the right side is a separate sulcus. The figs. 8 and 9 clearly show the condition which has been set out above, and they illustrate the difficulties of instituting exact homology even in the two hemispheres of the same brain. Taken as a whole, however, the frontal regions show a considerable degree of symmetry.

The Sulcus Præcentralis (5).—CUNNINGHAM in his Memoir describes three precentral sulci, superior, middle and inferior. The sulcus præcentralis superior has already been described with the sulcus frontalis superior. It is triradiate in form, being confluent with the element "α" of the sulcus frontalis superior.

The sulcus præcentralis medius (5*m*) is a definite sulcus in the higher anthropoids and Man and throws light on the expansion of the frontal region. In the Gibbon a small posteriorly directed branch arises from the point of maximum curvature of the arcuate-rectus complex. In the Orang this may appear as two branches, or a small sulcus may be extruded from the arcuate to lie between the sulcus præcentralis superior and the sulcus præcentralis inferior. This is the sulcus præcentralis medius. Turning to fig. 9 a condition is seen which is frequently seen in the brain of the Orang and Chimpanzee (see MINGAZZINI, 1928, fig. 9). There are two branches from the convexity of the sulcus præcentralis inferior which pass backwards and interlock with the lower limb of the sulcus præcentralis superior. These branches are sometimes completely extruded and constitute the sulcus præcentralis medius. The continuation of the sulcus præcentralis inferior (5*i*) is directed forwards into the gyrus frontalis medius. This anteriorly directed sulcus is homologous with the upper end of the sulcus arcuatus (ARC) in the apes. Essentially the same condition is seen on the left side, the only

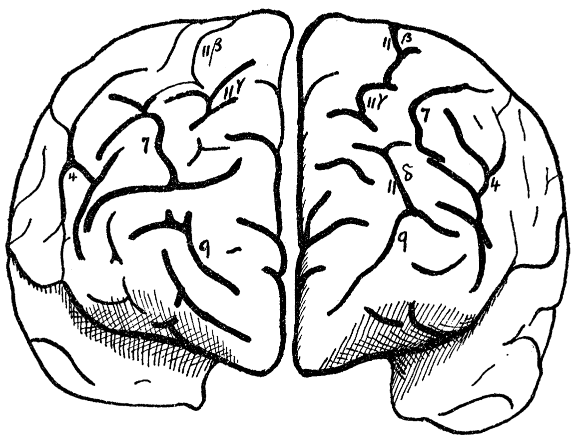

FIG. 24.—Line drawing of fig. 23, Plate 2.

difference being that the sulcus projecting into the middle frontal gyrus is somewhat shorter. The reasons for naming this sulcus the upper end of the arcuate are that its cortical relations show it as a sulcus between areas 6 and 8 of BRODMANN, and that the arrangement of the arteries in the Australian brain is the same at this point as it is at the upper end of the arcuate in monkeys. Such a diagrammatic representation of the arcuate sulcus in the human brain is unusual, for in most brains this upper end is detached. In some it may become confluent with, and be considered as, a part of the sulcus frontalis medius ; it may appear to be a part of the sulcus frontalis superior when this sulcus appears at a somewhat low level on the frontal lobe, or finally, it may be found as a separate sulcus. This interpretation of the sulcus arcuatus is very similar to that put forward by COLE.

Fig. 23, Plate 2, is a photograph of the anterior aspect of the brain of the Bushwoman and fig. 24 a line drawing of it. The rostral keel and the hollowed out appearance of the orbital border are well shown. On each side a well-marked sulcus passes obliquely forward almost to reach the frontal pole. This is the fronto-marginal sulcus of WERNICKE (9). The examination of frontal views of the Cercopithecidæ and of the higher apes reveals in practically every case this axial sulcus passing towards the frontal pole. In all of them it is an axial sulcus within area 10 of BRODMANN and in all of them it is a sulcus within an autonomous area of arterial supply from the fronto-polar branch of the anterior cerebral artery. Every criterion necessary for homology shows that this sulcus must be homologous with the anterior part of the sulcus rectus of monkeys. The posterior part of the sulcus rectus has cortical relations with area 9 of BRODMANN, and lies on the line of vascular demarcation between the anterior and middle cerebral arteries in this region. These conditions are frequently fulfilled by the anterior part of the sulcus frontalis medius (7). The pattern of the sulci, however, is so variable that it is not always possible to define the sulcus frontalis medius.

The Medial Surface of the Left Hemisphere. (Figs. 20, 21, 22.)

The Occipital Region.—The sulcus limitans præcunei (21*l*) arises from the calcarine sulcus at an angle of 60 degrees. It passes obliquely upwards and backwards to within one centimetre of the medial border of the hemisphere where it appears to divide into two branches. The interpretation of this region is dependent upon whether or not the anterior branch is confluent with the sulcus limitans præcunei. In many brains where the superior parietal lobule is complexly folded I have found that the operculum anterior fossæ parieto-occipitalis may be continued right on to the dorsal surface to include the sulcus intraparietalis; so that an extensive operculation may extend from the sulcus calcarinus on the medial surface to the sulcus intraparietalis on the lateral surface. In this hemisphere there does not appear to be an operculation of this nature. The apparent branch of a fissura parieto-occipitalis is in reality the inner end of the branch of the sulcus intraparietalis which bounds the arcus parieto-occipitalis anteriorly. It is probable that it is only superficially confluent with the sulcus limitans præcunei. The grounds for this view are (*a*) the lack of development of the upper part of the præcuneus, (*b*) the simplicity of pattern of the sulci of the præcuneus, (*c*) the identification of the sulci in the cuneus as the incisura parieto-occipitalis, the sulcus paracalcarinus and the sulcus limitans areæ striatæ superioris. The small posterior arm of what appears to be the fissura parieto-occipitalis is, if the above facts are valid, the upper end of the sulcus limitans præcunei. A series of Australian brains shows some which are very similar to this in which the operculum anterior fossæ parieto-occipitalis is only developed in its lower half. In higher forms the increased operculation leads to the covering of the incisura parieto-occipitalis and the sulcus paracalcarinus (21*p*) together with the arcus intercuneatus. When this occurs we get a simple linear fissura parieto-occipitalis. In the Bushwoman, the sulcus in the cuneus lying more or less parallel with the sulcus limitans præcunei, is the sulcus paracalcarinus (21*p*), having a distinctly simian form. Between the sulcus limitans præcunei and the sulcus paracalcarinus the incisura parieto-occipitalis (21*i*) is seen cutting the dorso-medial border of the hemisphere. The wedge of cortex lying between the sulci paracalcarinus and limitans præcunei and indented by the incisura parieto-occipitalis is the arcus intercuneatus here fully exposed. Fig. 22 shows the hypothetical reconstruction of the cortical areas founded on the work of ELLIOT SMITH and dependent upon the above interpretation of the sulcal pattern. It is extraordinary how similar this cortical reconstruction is to the cortical chart described by ELLIOT SMITH, not only for the occipital region, but also for the whole medial surface: the sulci almost exactly correspond. Professor ELLIOT SMITH informs me that his picture was made from the medial surface of the brain of a negro and that the sulci and cortical areas were drawn in at one sitting. He remembers that the cortical areas were exceptionally distinct on account of the pigmentation of the cortex.

The sulcus retrocalcarinus (20) is horizontally disposed. Posteriorly it divides into two branches which reach the occipital pole. Well-marked sulci limitantes areae striatæ superioris et inferioris are present.

The Sulcus Cinguli (10).—EBERSTALLER divided the sulcus cinguli into three parts. In the aboriginal Australian I find the sulcus cinguli in three separate parts in 36% of cases, in two parts in 24% of cases and continuous as one sulcus in 24% of cases. RETZIUS in the European found 14% in the first group, 44% in the second and 41% in the third; in the Chinese I find the percentages in the three groups 6, 22 and 72 respectively.

In the aboriginal Australian, not only is there a greater percentage of brains where the parts of the sulcus cinguli are separate, but there is also an absence of, or a lesser development of, those compensatory sulci between the sulcus cinguli and the dorsal border of the hemisphere which are named by ELLIOT SMITH the paracingular sulcus, and there is also an absence of sulci radiating towards the dorsal border.

The same evidences of lack of development of the medial part of the frontal lobe are all present in the brain of the Bushwoman. The sulcus cinguli (10) is separated into three parts. The anterior part commences under the genu of the corpus callosum and, passing forwards and slightly upwards, ends by turning sharply upwards into the sulcus suprarostralis. The anterior part is morphologically distinct from the remainder of the sulcus. It forms the boundary between the areas fronto-polaris and frontalis superior A of ELLIOT SMITH, areas 11 and 10 of BRODMANN. The middle part of the sulcus cinguli in this brain is a simple sulcus which lies parallel with the anterior two-thirds of the corpus callosum. It is placed between the callosal areas B and C and the area frontalis D of ELLIOT SMITH, areas 24 and 32 of BRODMANN. The posterior part is also genetically and morphologically distinct from the remainder of the sulcus. In this brain it is branched anteriorly on account of either deep or superficial connections with the paracentral sulci of the paracentral lobule. The arrangement of the paracentral sulci is almost exactly the same as that depicted by ELLIOT SMITH (1907, fig. 3). The area postcentralis is limited posteriorly by the upper end of the third part of the sulcus cinguli; anteriorly, a branch of the sulcus paracentralis occupies a position which places it at the anterior limit of this area. Anterior to this the remainder of the paracentral sulcus bisects the paracentral lobule and lies between areas præcentralis A and B. The paracentral lobule is bounded anteriorly by the sulcus præparacentralis.

The Sulcus Paracingularis is represented by shallow branching sulci lying between the sulcus cinguli and the dorsal border (29).

The Sulcus Subrostralis lies below and parallel with the first part of the sulcus cinguli. It is the boundary between the areas præfrontalis and fronto-polaris of Elliot Smith.

It is evident that the medial surface of the hemisphere shows in practically every area a primitiveness of structure which is entirely in keeping with the pattern of the sulci on the lateral surface of the hemisphere.

Summary.

The study of this brain, so ably described by Marshall, in the light of the newer knowledge gained from recent studies, focuses attention on certain areas which attracted the special notice of Flechsig, Brodmann, Campbell, Elliot Smith and Head. These areas of late myelinization, advanced cytoarchitectonic differentiation, extreme clinical and psychological interest, have also attracted attention from the point of view of the individuality of their vascular supply. The cortical areas in the brain of the Bushwoman which are primitive as judged by the sulcal pattern in comparison with the brains of the aboriginal Australian and Chinese are :—

(1) The occipital region which presents on both sides a wide lateral extension of the area striata with fully developed sulci lunati and intrastriate sulci of primitive form, curved and clearly defined sulci occipitales anteriores ; and on the medial surface of the left hemisphere an exposed arcus intercuneatus indicating a failure in development of the cuneal and precuneal areas. The pattern of the sulci is so clear that hypothetical cortical charts can be reconstructed.

(2) The parietal region in which the form of the branching of the posterior part of the parallel sulcus is directly comparable with that seen in many Gorilla and Chimpanzee brains, in which the sulcus intraparietalis is relatively simple in its foldings and in which the sulci of the superior parietal lobule are simple. The main expansion of this area appears to have taken place in the region of the supramarginal lobule.

(3) The temporal lobe is narrow and lacks fulness. Anteriorly the temporal pole is narrow and slender and fails to extend forward to cover the posterior part of the orbital surface of the frontal lobe. Associated with the general under-development of the temporal lobe is the exposed condition of the island of Reil on both sides.

(4) The frontal region which shows primitive features of both form and sulcal pattern. Marshall emphasized the peculiar narrowing of the frontal lobes, with prominent antero-external angles. In this respect the form of the brain of the Bushwoman is very similar to that of *Pithecanthropus*. The sulcal pattern is so simple in arrangement

that there is little doubt of the correctness of the homologies of the sulcus arcuatus and sulcus rectus. On the medial surface the broken condition of the sulci indicates the same lack of development of the frontal lobe.

EXPLANATION OF THE NUMBERS IN THE FIGURES.

1. s. subfrontalis.
2*a*. ramus ascendens fissurae Sylvii.
2*h*. ramus horizontalis fissurae Sylvii.
4. s. frontalis inferior.
4*a*. ramus anterior s. frontalis inferior.
5*i*. s. præcentralis inferior.
5*m*. s. præcentralis intermedius.
5*s*. s. præcentralis superior.
7. s. frontalis medius.
9. s. fronto-marginalis. (s. rectus).
10. s. cinguli.
11. s. frontalis superior.
12. s. subcentralis.
13. s. diagonalis.
14. s. centralis.
15*i*. s. postcentralis inferior.
15*s*. s. postcentralis superior.
16. s. intraparietalis.
17. s. occipitalis transversus.
18. s. lunatus.
18*d*. pars dorsalis sulci lunati.
18*v*. pars ventralis sulci lunati.
18*p*. s. prælunatus.
19. s. calcarinus externus.
19*a*. s. accessorius calcarinus externus.
20. s. retrocalcarinus.
21. f. parieto-occipitalis.
21*l*. incisura parieto-occipitalis.
21*l*. s. limitans præcunei.
21*p*. s. paracalcarinus.
22. s. paramesialis.
23. s. parallelus.
24. s. parallelus superior vel supramarginalis.
25. s. angularis.
26. s. occipitalis anterior.
27. s. temporalis medius.
29. s. paracingularis.
30. s. subparietalis.
31. s. præcunei.
ARC. s. arcuatus.

REFERENCES.

Anthony, R. et Santa-Maria, A. S. de, 1912. 'Bull. Soc. Anthrop. Paris,' vol. **3**, p. 293.

Bolton, J. S., 1914. "The Brain in Health and Disease." London.

Brodmann, K., 1909. "Vergleichende Lokalisationslehre der Grosshirnrinde." Leipzig.

Cunningham, D. J., 1982. 'Roy. Irish Acad. Mem.,' No. 7.

Flashman, J. F., 1908. 'Rep. Path. Lab. Lunacy Dept., N.S.W. Government, vol. **1**, part 3.

Genna, G. E., 1924. 'Riv. Anthrop.' vol. **26**.

Gratiolet, P., 1854. "Memoire sur les plis cerebraux de l'homme et des Primates." Paris, p. 65.

Harris, H. A., 1928. 'Univ. Coll. Hosp. Mag. Lond.,' vol. **13**, No. 3, p. 84.

Ingalls, N. W., 1914. 'J. Comp. Neurol.,' vol. **24**, p. 201.

Jefferson, G., 1913. 'J. Anat.,' vol. **47**, p. 365.

Kappers, C. U. Ariëns, 1929. "The Evolution of the Nervous System in Invertebrates, Vertebrates and Man." Haarlem.

Karplus, J. P., 1902. 'Arbeit. neur. Inst. Univ. Wein.' vol. **9**, p. 118.

—— 1905. *Idem*, vol. **12**, Pl. 1.

KEITH, A., 1931. "New discoveries relating to the antiquity of Man." London.

KOCH, J. L. A., 1867. "Ueber das Hirn eines Buschweibes." Tubingen.

MARSHALL, JOHN, 1864. 'Phil. Trans.' vol. **154**, p. 501.

MINGAZZINI, G., 1928. 'Arch. Psychiat. Nervenkr.,' vol. **85**, p. 1.

SHELLSHEAR, J. L., 1927. 'J. Anat.,' vol. **49**, p. 267.

—— 1930. *Idem*, vol. **45**, p. 45.

SMITH, G. ELLIOT, 1904. "Studies in the morphology of the human brain." No. 1. "The occipital region." 'Rec. Egypt. Govt. Sch. Med.,' vol. **2**, p. 125.

—— 1907. 'J. Anat.,' vol. **41**, p. 237.

—— 1927. "The Evolution of Man." 2nd Edition, Oxford.

TIEDEMANN, 1870. 'Abhand. Bayer. Akad. Wiss.,' vol. **10**, p. 388.

SLOME, ISIDORE, 1932. 'J. Anat.,' vol. **67**, p. 47.

DESCRIPTION OF PLATES.

PLATE 1.

FIG. 1.—Photograph of the ventral surface of the brain of the Bushwoman. The greatest antero-posterior length of the original, marked full size, is 5·8 inches; the greatest width is 4·6 inches. MARSHALL's measurements taken by the aid of intracranial casts are:—extreme length 6·6 inches, extreme breadth 5·1 inches.

FIG. 3.—Photograph of the dorsal surface of the brain of the Bushwoman.

PLATE 2.

FIG. 6.—Copy of MARSHALL's photograph of the posterior aspect of the Bushwoman's brain, hitherto unpublished.

FIG. 11.—The photograph from which fig. 8 is drawn.

FIG. 12.—The photograph from which fig. 9 is drawn.

FIG. 23.—Photograph of the brain from the frontal aspect.

PLATE 3.

FIG. 17.—The lateral view of the brain of an aboriginal Australian from the Institute for Brain Research at Amsterdam, to show the sulci of the inferior parietal lobule.

FIG. 20.—The photograph of the left medial surface of the left hemisphere of the Bushwoman's brain.

FIG. 25.—Copy of MARSHALL's photograph showing the brain *in situ*.

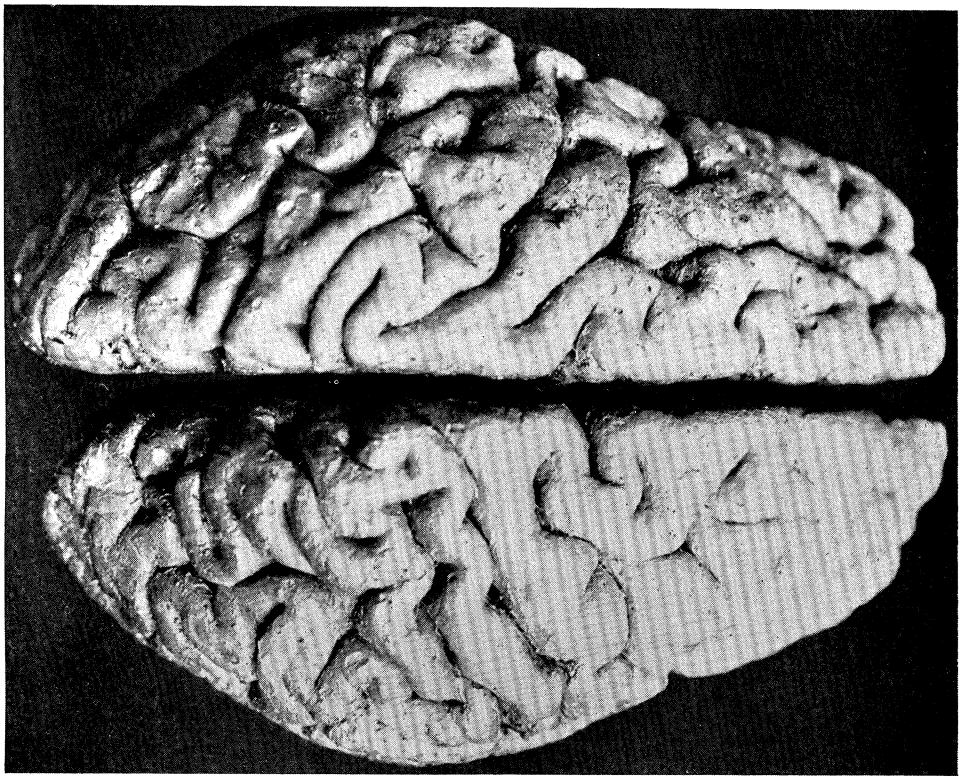

Fig. 3.

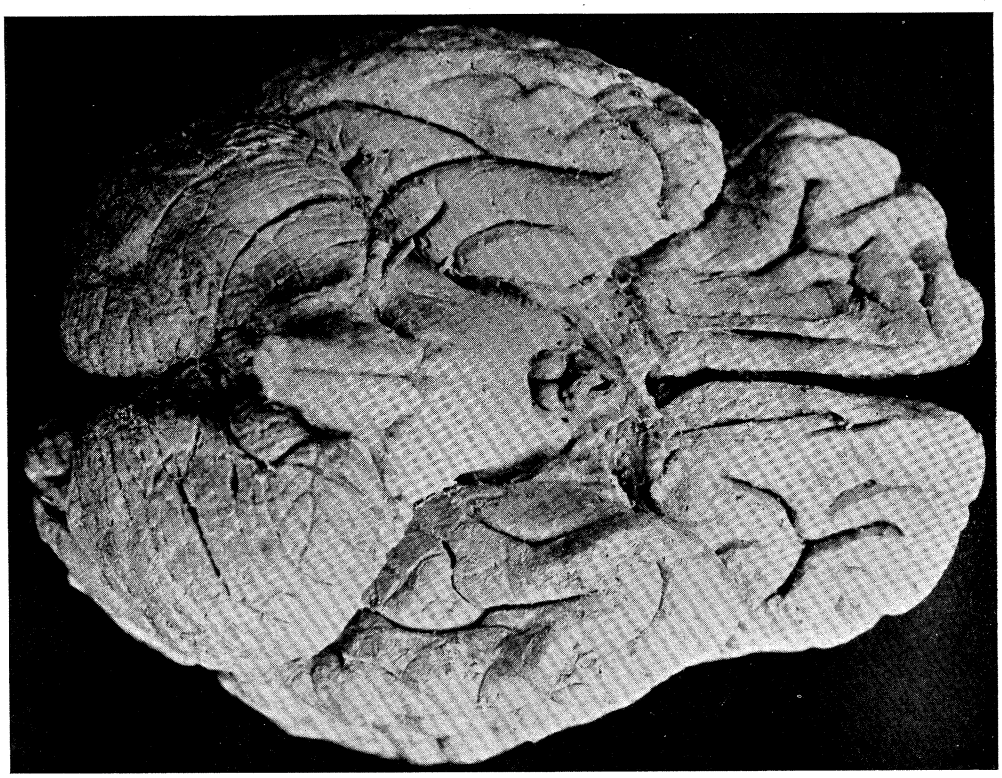

Fig. 1.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

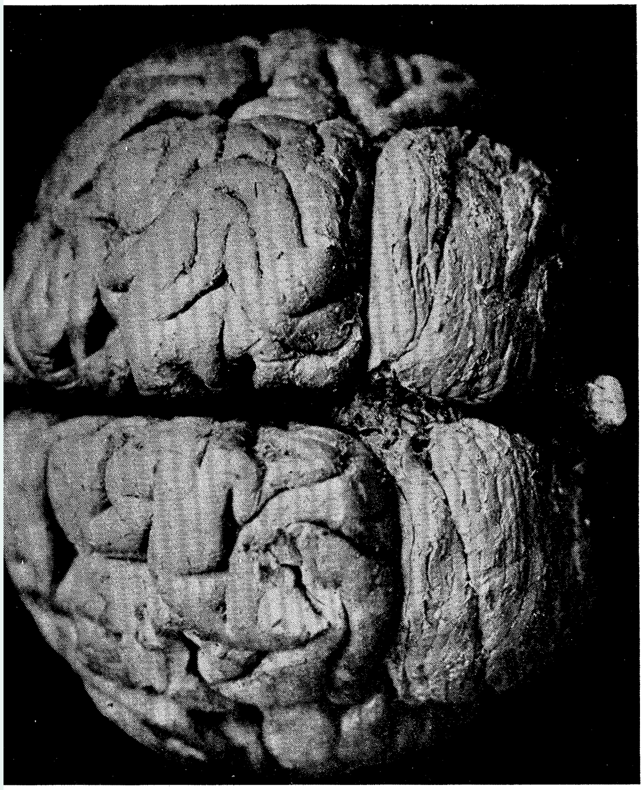

Fig. 6.

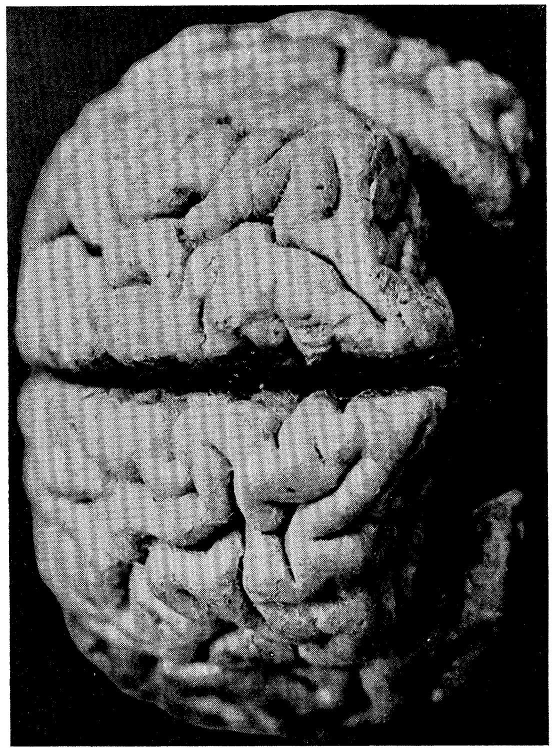

Fig. 23.

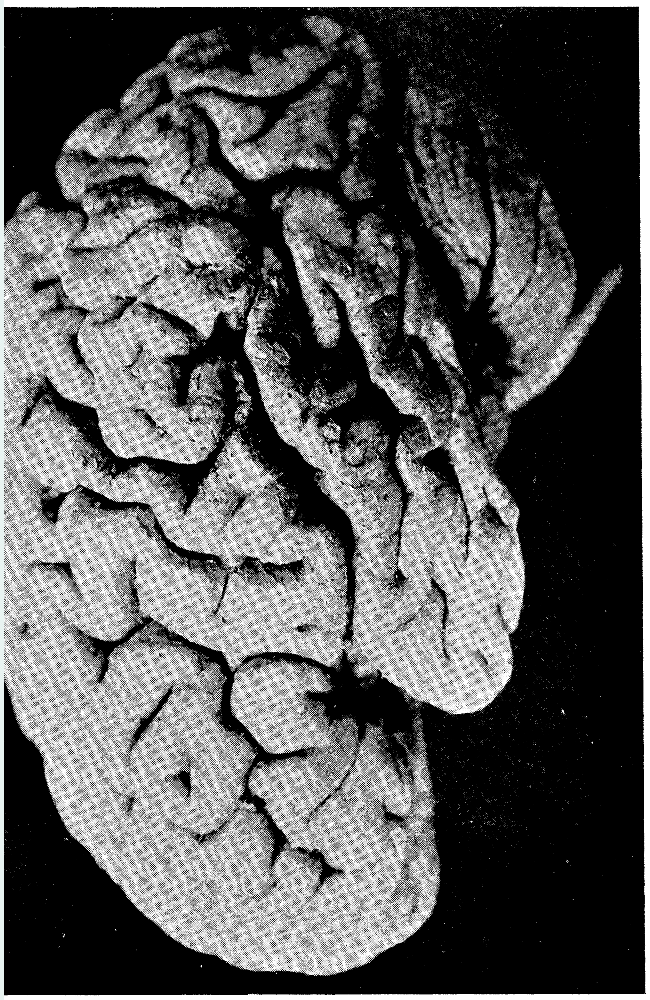

Fig. 11.

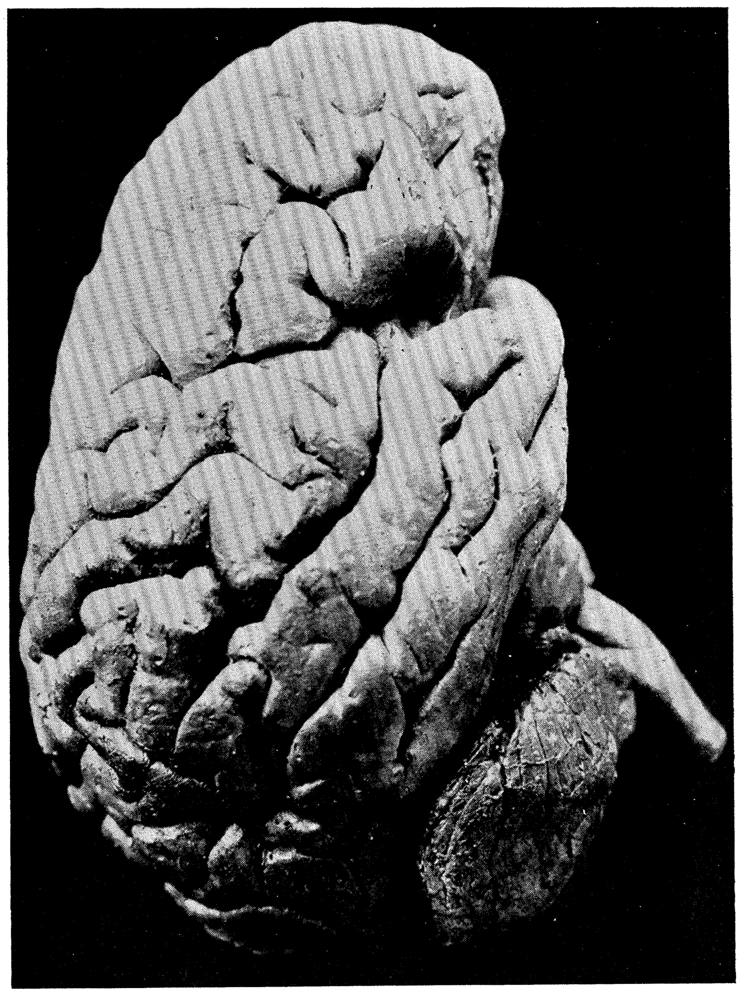

Fig. 12.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

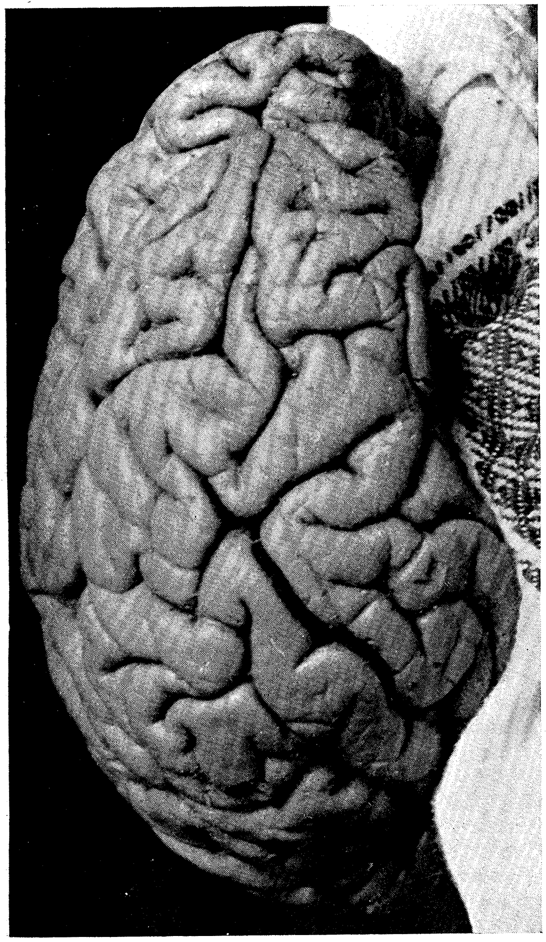

Fig. 17.

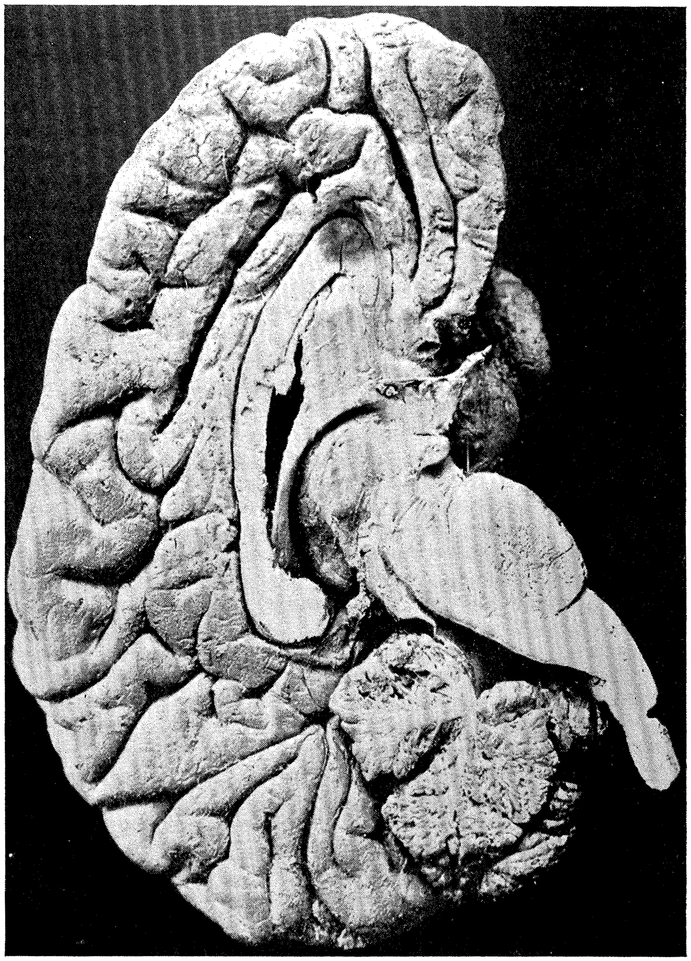

Fig. 20.

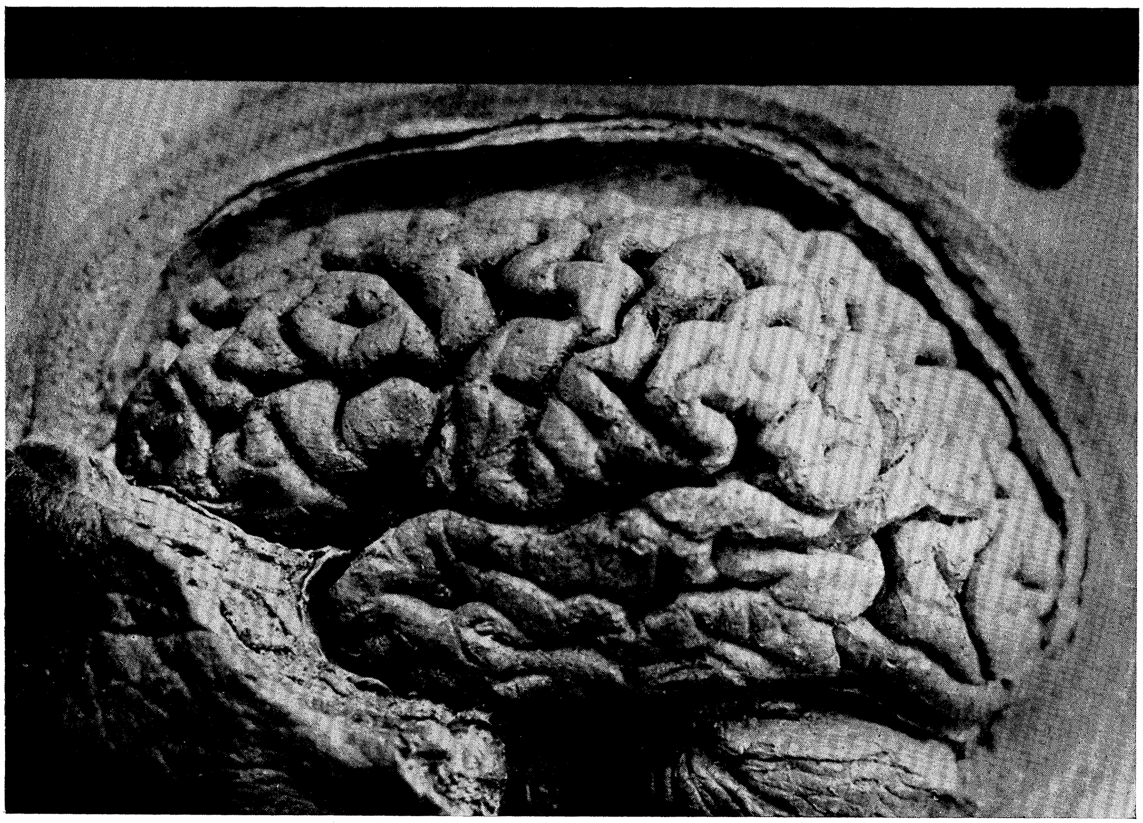

Fig. 25.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

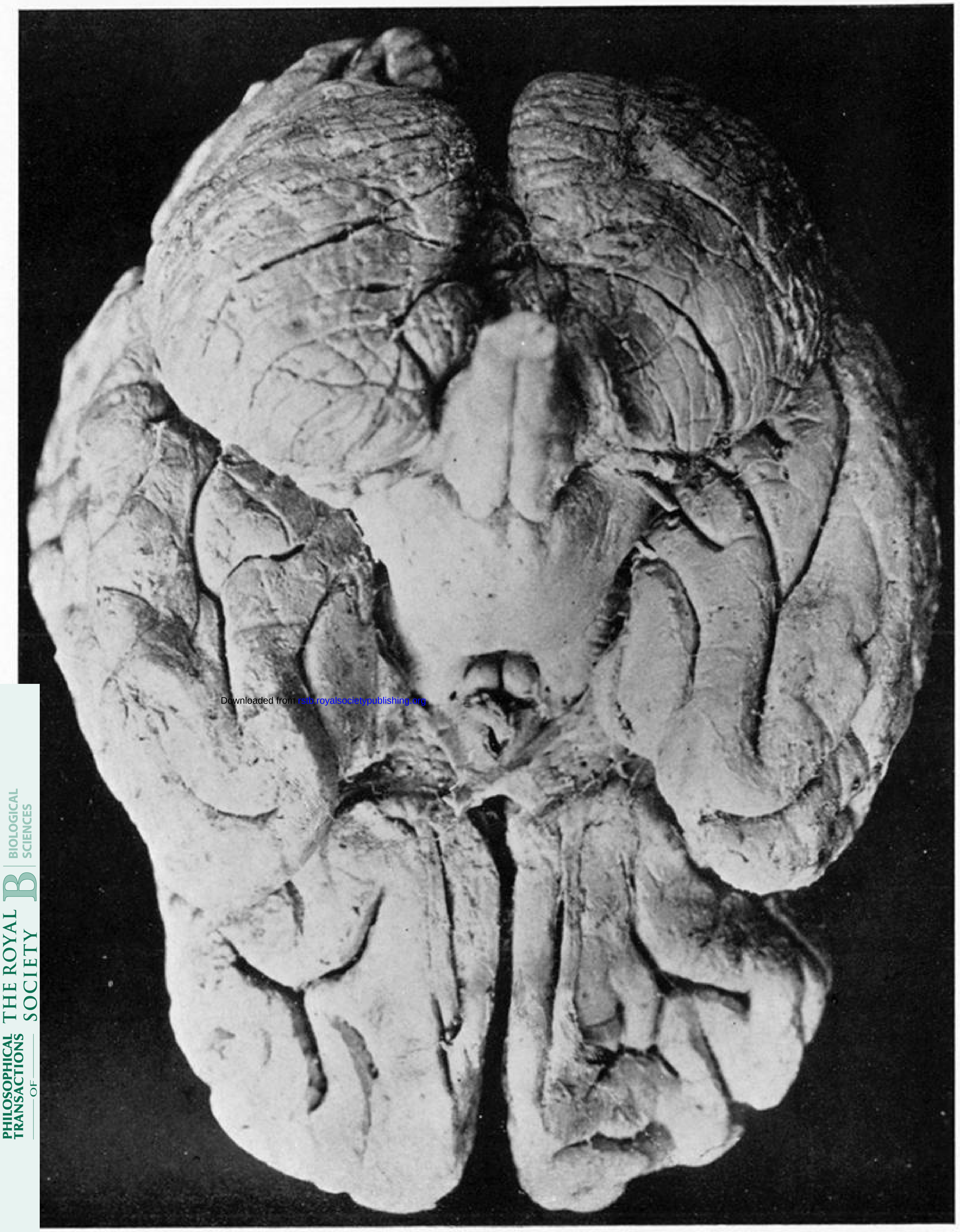

Fig. 1.

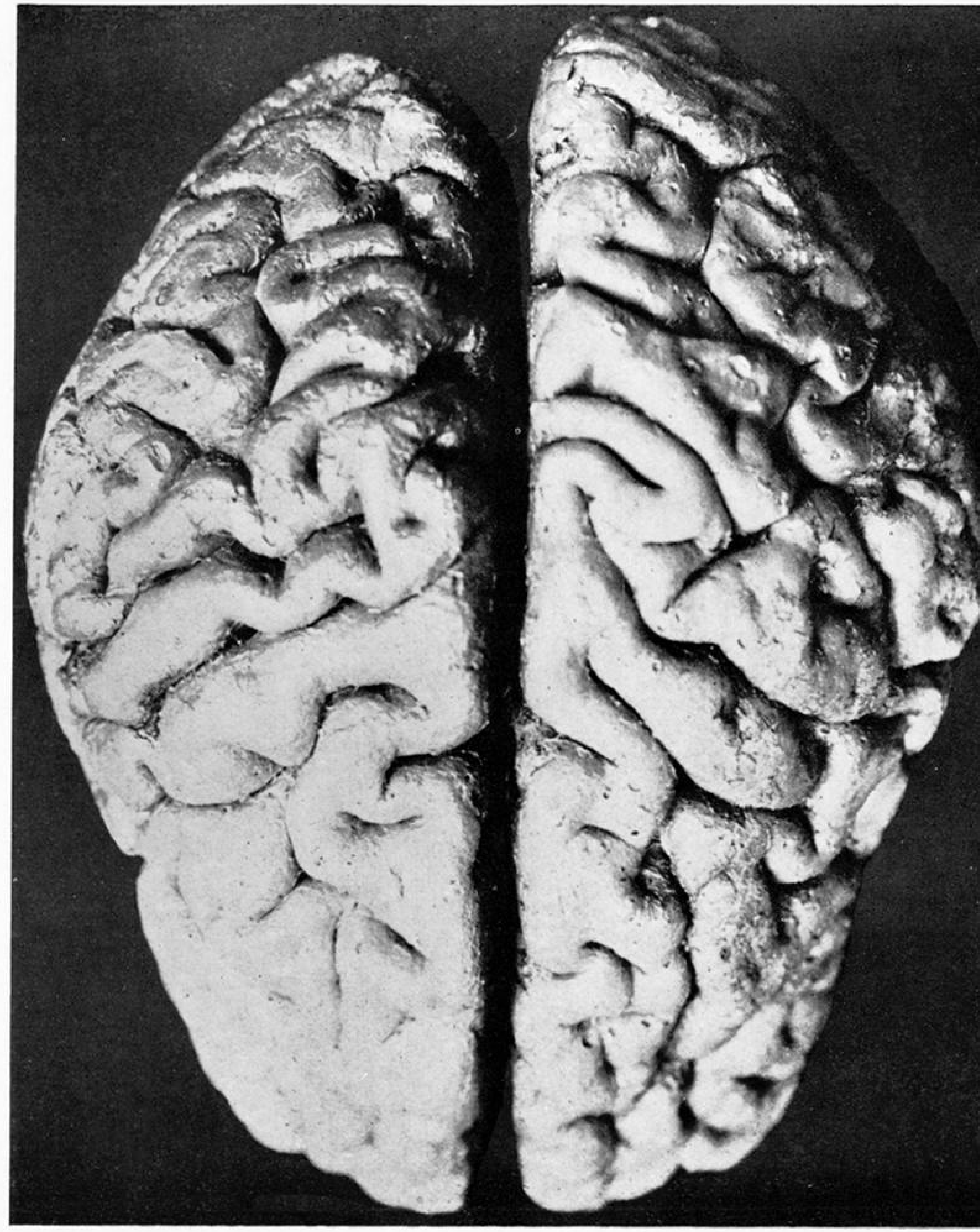

Fig. 3.

Plate 1.

Fig. 1.—Photograph of the ventral surface of the brain of the Bushwoman. The greatest antero-posterior length of the original, marked full size, is 5·8 inches; the greatest width is 4·6 inches. Marshall's measurements taken by the aid of intracranial casts are:—extreme length 6·6 inches, extreme breadth 5·1 inches.

Fig. 3.—Photograph of the dorsal surface of the brain of the Bushwoman.

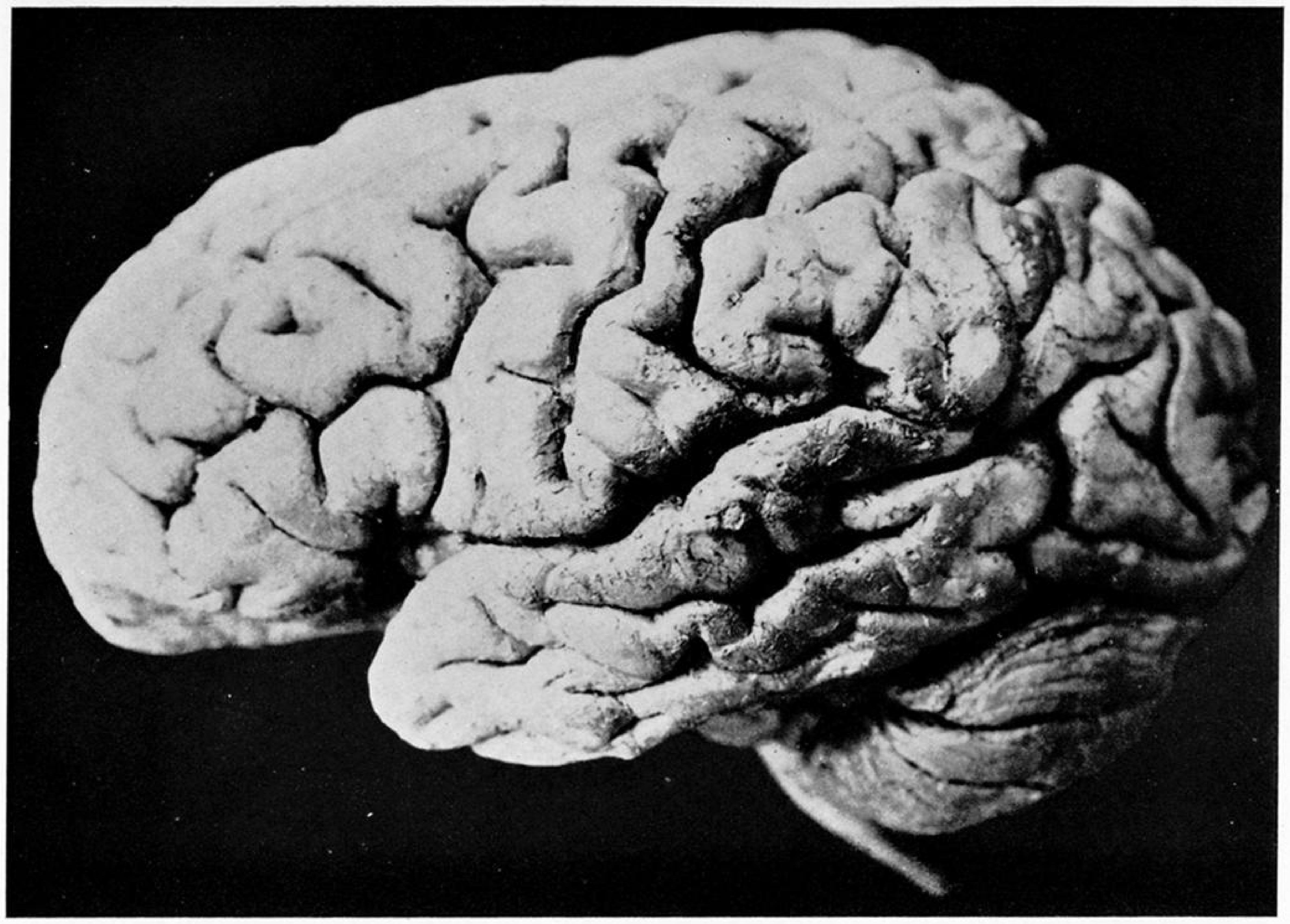

Fig. 11.

Fig. 6.

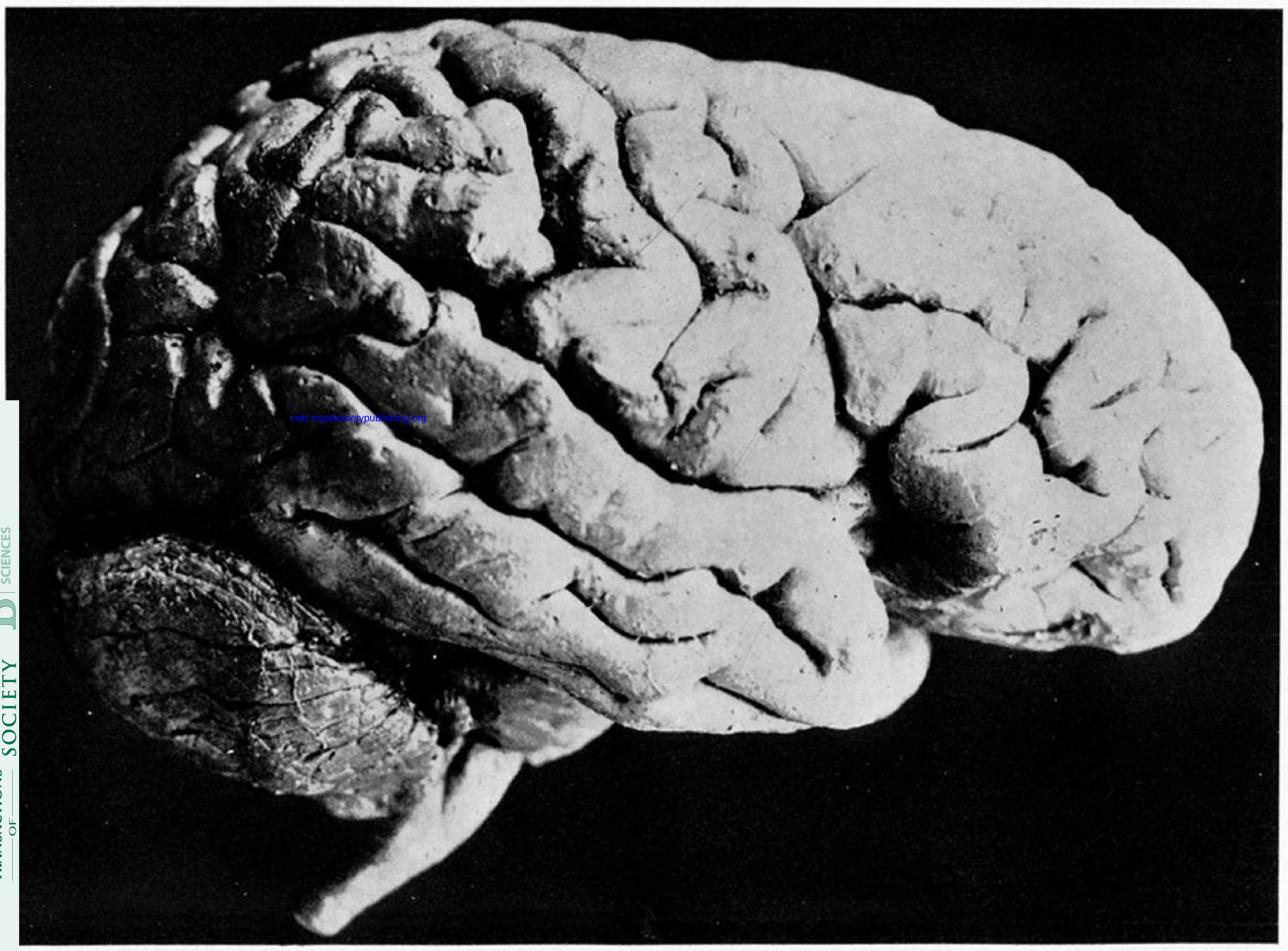

Fig. 12.

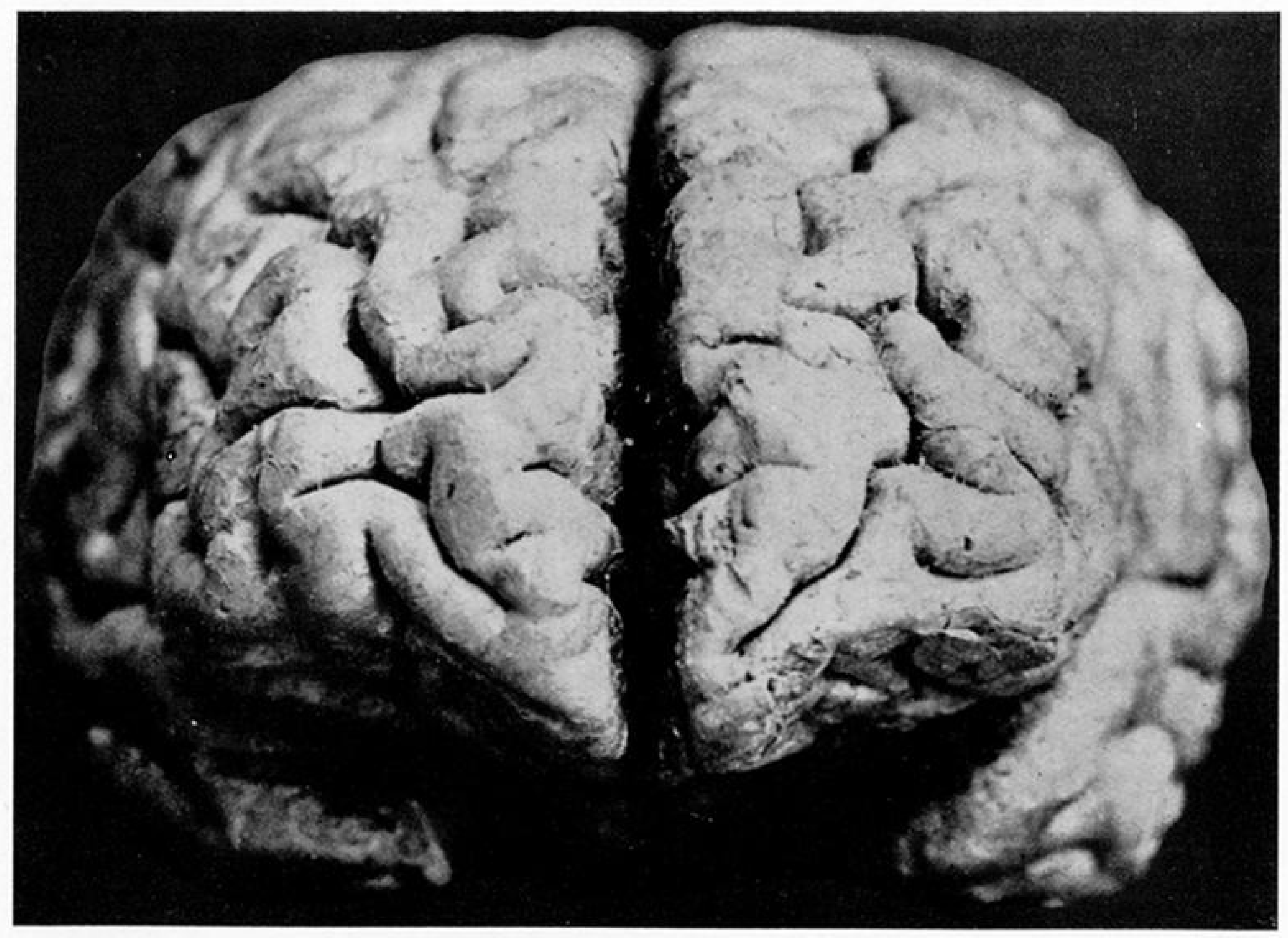

Fig. 23.

Plate 2.

Fig. 6.—Copy of Marshall's photograph of the posterior aspect of the Bushwoman's brain, hitherto unpublished.

Fig. 11.—The photograph from which fig. 8 is drawn.

Fig. 12.—The photograph from which fig. 9 is drawn.

Fig. 23.—Photograph of the brain from the frontal aspect.

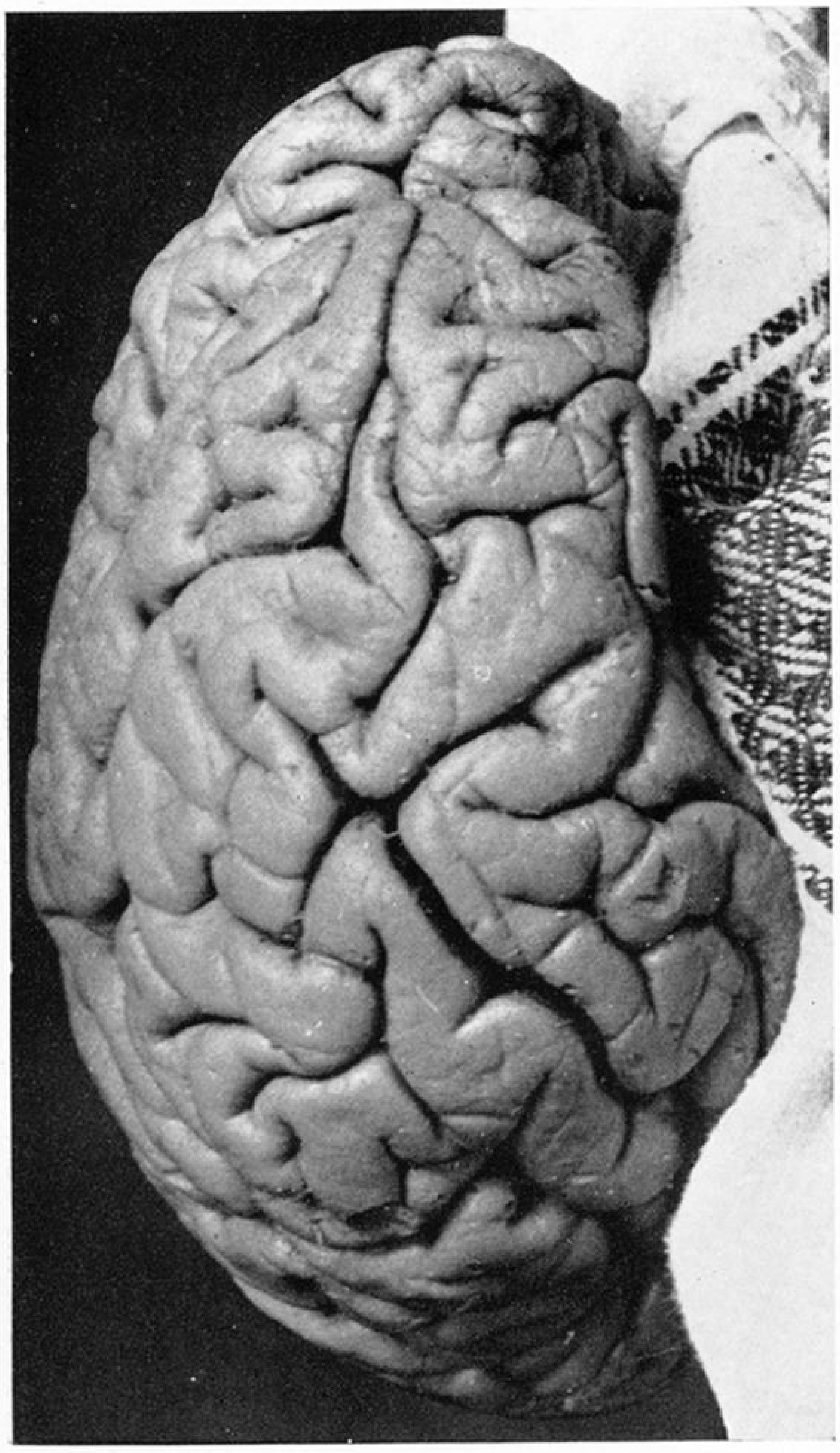

Fig. 17.

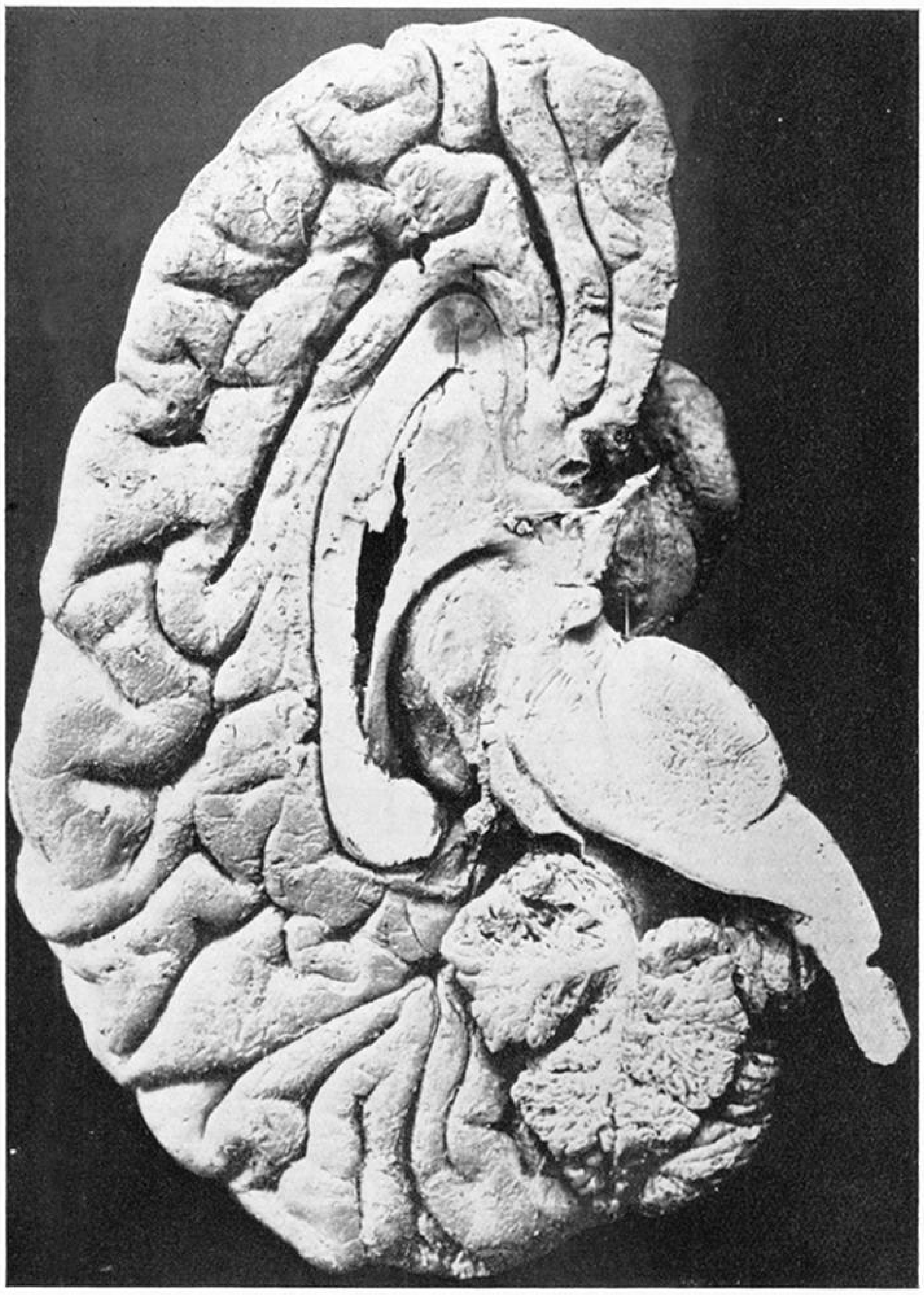

Fig. 20.

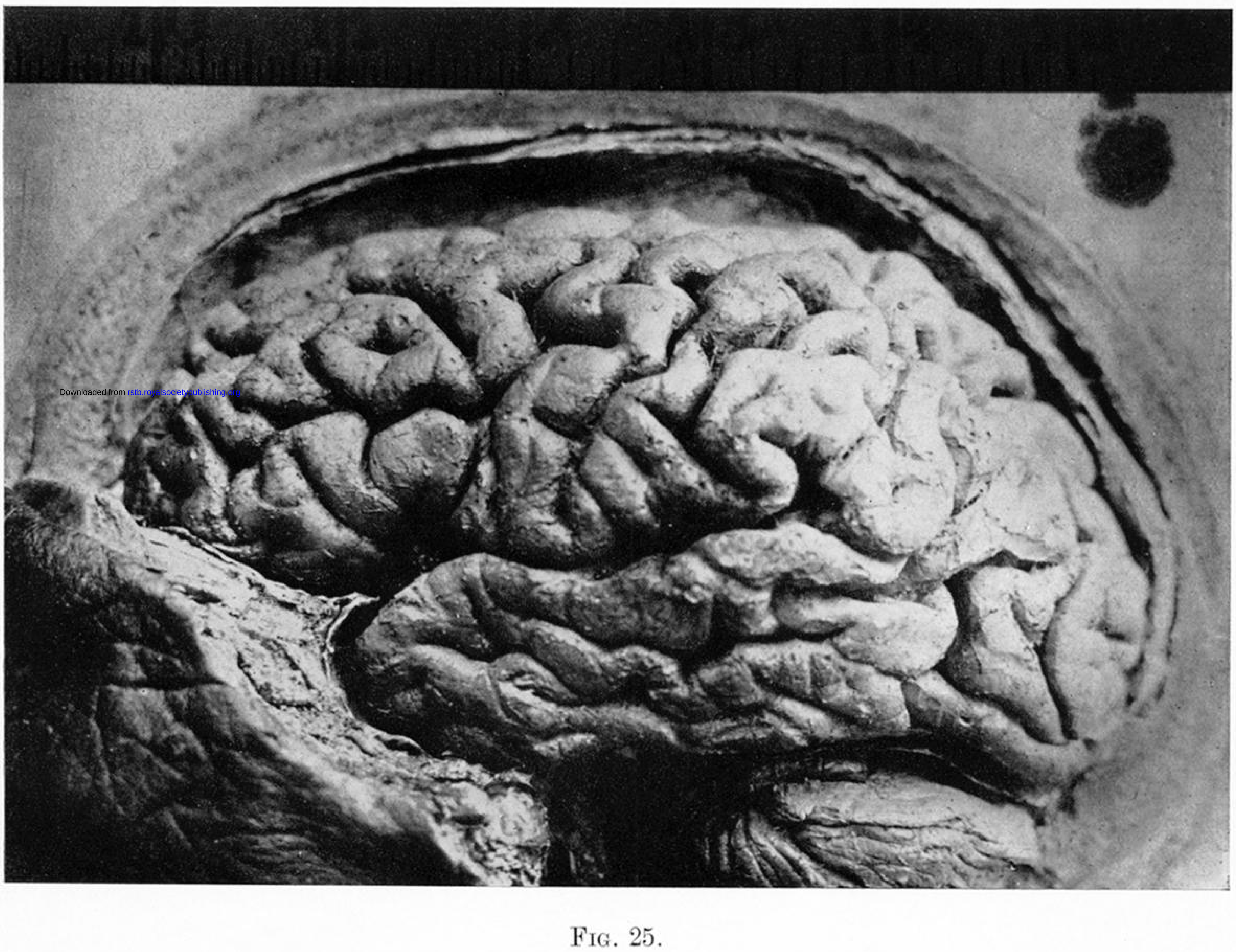

Fig. 25.

Plate 3.

Fig. 17.—The lateral view of the brain of an aboriginal Australian from the Institute for Brain Research at Amsterdam, to show the sulci of the inferior parietal lobule.

Fig. 20.—The photograph of the left medial surface of the left hemisphere of the Bushwoman's brain.

Fig. 25.—Copy of Marshall's photograph showing the brain *in situ*.