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ON

THE STRUCTURE

OF

THE BRAIN IN MARSUPIAL ANIMALS.

BY

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VIII. *On the Structure of the Brain in Marsupial Animals.* *By* RICHARD OWEN, *Esq. F.R.S. Hunterian Professor of Anatomy to the Royal College of Surgeons.*

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THE brain in Mammalia is essentially characterized by the complexity and magnitude of the apparatus by which its different masses are brought into communication with one another. With respect to size, the cerebral hemispheres are in many species proportionally inferior to those of Birds; and in most Insectivorous and Rodent Mammalia they present an equally smooth and uniform external surface; but notwithstanding the absence of convolutions and diminished size of the cerebral hemispheres in such Mammalia, a large apparatus of medullary fibres is present, which connect together either the opposite hemispheres, or the distant parts of the same hemisphere; and this apparatus, or great commissure, is superadded to the anterior, posterior, and soft commissures, which, with the exception of a very slight rudiment of the fornix, are alone developed in birds for the purpose of uniting the opposite hemispheres. In the higher Mammalia, in which the cerebral hemispheres acquire superior size and increased extent of surface by means of convolutions, the superadded commissural apparatus presents a corresponding development and a highly complicated structure; its several parts being distinguished as the corpus callosum, fornix, and their intercommunicating laminæ, termed the septum lucidum. The fornix, by means of its posterior crura and the intermediate medullary tract termed the lyra, brings the hippocampi majores into communication with each other, and with the posterior folds of the corpus callosum*; by means of its anterior crura it establishes a communication between the hippocampi and the optic thalami; and by means of the septum lucidum its connexion with the corpus callosum is continued to the anterior fold of that body†.

In the Human brain the fornix, though of complex structure and developed as a very distinct part, is of small size as compared with the corpus callosum; while the delicate

* "The fasciculi from the fornix form in part the covering of the hippocampus, and in part its loose fold, the tænia hippocampi."—REIL in MAYO's Anatomical Commentaries, p. 116.

"L'envelope medullaire de la corne d'Ammon se continue avec la partie posterieure du corps calleux, et en partie aussi avec le pilier posterieur de la voute: c'est dans ce dernier que va se jeter le corps frangé tout entier."—MECKEL, *Anatomie Descript.* tom. ii. p. 679.

† "Ainsi la voute represente une chaine très complexe qui unit les deux hémisphères l'un avec l'autre sur plusieurs points, et qui, de plus, établit une communication entre la partie anterieure et la partie posterieure de chaque hémisphère."—MECKEL, *Anatomie Descript.* tom. ii. p. 658.

laminæ of the septum lucidum by which the fornix is connected with the corpus callosum, present an extent of surface corresponding to the degree to which the corpus callosum and fornix recede vertically from one another as they advance from behind forwards. In tracing the modifications of these different parts through the mammiferous series, the disproportion of the fornix to the corpus callosum is found to decrease as the parts, to the connexion of which they are subservient, alter in their relative size. For as the superincumbent masses of the cerebral hemispheres diminish in the placental Mammalia, the corpus callosum is proportionally restricted in its development; while the hippocampi and their free processes, called the tæniæ hippocampi, maintaining a remarkable uniformity in their absolute size, the fornix also continues large, and undergoes modifications of form which more distinctly manifest its relation as a commissure to the hippocampi than its structure in the human brain would indicate. Thus in the brain of the Sheep the tæniæ hippocampi, instead of being lost in the posterior crura of the fornix, are continued along its lateral margins, augmenting its breadth: they converge and unite above the anterior crura of the fornix, which here appear as small subordinate appendages sent off into the optic thalami below, from the union of the tæniæ above; the tæniæ are then again separated and are continued downwards and forwards into the anterior lobes of the hemispheres, bringing these parts into communication with the hippocampi behind, whilst the point of union of the opposite tæniæ becomes continuous with the anterior fold of the corpus callosum above.

As the corpus callosum and fornix recede vertically from one another in a less degree in most Mammalia than in Man, the two laminæ of the septum lucidum are consequently of less extent, but are proportionally stronger; they are formed not merely by the epithelium of the lateral ventricles, but by fibrous laminæ extending from the anterior and upper surface of the fornix to the opposite surface of the corpus callosum. In the simple and depressed forms of brain, such as the Rodentia present, the fornix, or hippocampal commissure, and the corpus callosum, or hemispheric commissure, are in contact, so that their uniting medium cannot with propriety be termed the septum lucidum.

The corpus callosum is the principal bond of union between the opposite hemispheres, extending horizontally above the ventricles, its middle fibres passing transversely, while those of its extremities, which are more or less bent beneath its body, radiate, and all intermix, in apposition with the ascending and diverging fibres of the peduncles of the cerebral hemispheres. It has hitherto been considered as the great characteristic of the brain in the Mammalia, and, taking the human brain as the term of comparison, to be developed in the ratio of the magnitude of the cerebral hemispheres.

In the placental Mammalia this is a pretty accurate expression of the relations of the corpus callosum; and as the posterior lobes of the hemispheres are the first to disappear in the descending comparison, so the corpus callosum diminishes in longitudinal extent from behind forwards, and thus the corpora quadrigemina, pineal gland, and posterior part of the optic thalami are successively brought into view on divaricating the cerebral hemispheres in the different Mammalia which exhibit this progressive degradation of the great commissure.

The researches of Tiedemann, as is well known, have shown that the anterior part, which is the most constant in the mammiferous series, is that from which the development of the corpus callosum commences in the human brain.

The aim of the present paper is not, however, to trace step by step the various modifications of the commissural apparatus of the hemispheres through the mammiferous class, but is limited to the description of a remarkable modification in that apparatus in the brains of the marsupial animals, to the detection of which I was led by observing that the commissural system presented the essential difference between the brains of the oviparous and mammiferous Vertebrata, and by associating the greater perfection of the brain, resulting from the development of the great commissure with the placental mode of development in the true Mammalia.

The connexion subsisting between placentation and high cerebral organization may be one of simple coincidence, yet it is certain that of all the great organic systems, the cerebral or sentient organ is that which alone offers a marked improvement of gradational structure in the animals developed by a placenta.

An attentive study of the manners of different Marsupiata in confinement, and an inspection of the exterior forms of the brain in some of the species, induced me to allude in a former paper to an inferiority of intelligence and a low development of the cerebral organ as being the circumstances in the habits and structure of these singular animals which were most constantly associated with the peculiarities of their generative economy*. I have since derived the most satisfactory confirmation of this coincidence from repeated dissections of the brains of Marsupiata belonging to different genera; and although unable to explain how a brief intra-uterine existence and the absence of a placental connexion between the mother and fœtus can operate (if it be really effective) in arresting the development of the brain, yet it is a coincidence which has been so little suspected, and is so interesting in various points of view, that I believe the evidence of it will be acceptable both to the physiologist and the naturalist.

In order to obtain satisfactory proof of the difference in the structure of the brain in the marsupial and placental quadruped, I dissected and compared together, step by step, the brains of a Wombat and Beaver. These animals, as is well known, are of nearly similar bulk, and manifest so many mutual affinities in their structure, that they have been, ~~and still are,~~ by some naturalists, classed in the same order of Mammalia. The Wombat is, in fact, in all its exterior characters, save the marsupial pouch, a Rodent; and in its internal anatomy, especially its digestive organs, more nearly resembles the Beaver than do many of the true rodent animals. The

* Philosophical Transactions, 1834, p. 358.

brain of the Beaver was also preferred for this comparison of internal organization, because on an outward inspection it would be pronounced to be the less highly organized of the two; the hemispheres in the Wombat presenting a few convolutions (Plate V. fig. 3.), whilst in the Beaver they are perfectly smooth (Plate V. fig. 1.).

In the Beaver, however, the cerebrum is extended further backward, though still leaving the cerebellum quite uncovered; while in the Wombat a portion of the optic lobes (corpora quadrigemina) is also exposed.

On divaricating the hemispheres of the brain in the Beaver, we bring into view, about three lines below the surface, the corpus callosum; and on removing the cerebral substance to a level with this body, its fibres are observed to diverge into the substance of each hemisphere, in the usual manner, some bending upwards, but a greater proportion arching downwards, and embracing the cerebral nuclei; the anterior fibres radiating into the anterior, the posterior fibres into the posterior extremities of the hemispheres. (Plate VI. fig. 3.)

The portions of the brain which are removed in thus tracing the extent of the corpus callosum, bring into view the corpora bigemina and the pineal gland; but the optic thalami are concealed by the great commissure above described.

On separating the hemispheres of the brain of the Wombat, not only the bigeminal bodies and pineal gland, but the optic thalami are immediately brought into view, and instead of a broad corpus callosum, we perceive, situated deeply at the bottom of the hemispheric fissure, a small commissural medullary band, *m*, (Plate VII. fig. 4.) passing in an arched form over the anterior part of the thalami, and extending beneath the overlapping internal or mesial surfaces of the hemispheres, which thus appear, as in the Bird, to be wholly disunited.

On gently raising the hemispheres from above the commissure, and pressing them outwards with the handle of a scalpel, the instrument passes into the fissure upon which the hippocampus is folded; and on continuing the pressure the hippocampus is torn through, and the lateral ventricle is exposed. The mesial wall of the hemisphere is continued from the superior and internal border of the hippocampus, and is composed in the Wombat, as in the Bird, of a thin lamina of medullary substance analogous to the septum lucidum. In the Kangaroo, the mesial parietes of the lateral ventricles are stronger, being about two lines in thickness.

The posterior transverse fibres of the commissure are continued outwards and backwards, beneath the more longitudinal fibres, which overlap them as they pass from the tæniæ hippocampi forwards to the anterior cerebral lobes. All the fibres of the commissure pass along the floor of the lateral ventricles into the substance of the hippocampi majores, which are of proportionally very large size. (See Plate VI. and VII. fig. 4, *n*.)

Thus the commissure which is brought into view on divaricating the cerebral hemispheres in the Wombat is seen to be partly the bond of union of the two hippocampi majores in the transverse direction, and partly of the hippocampus and anterior lobe of the same hemisphere in the longitudinal direction. It also fulfils the other function of the fornix by sending down from the inferior surface two small nerve-like processes, which extend vertically, behind the anterior commissure, through the substance of the optic thalami, near their mesial surfaces, to the corpus albicans, at the base of the brain.

The superior view of the connexions of the hippocampal commissure of the Wombat is given at Plate VI. fig. 4.

Returning to the Beaver's brain, we raise the posterior thickened margin of the corpus callosum, ~~and~~ at the middle of its inferior surface we find it closely connected with the centre of a commissural band of fibres, arching over the anterior part of the optic thalami, and passing outwards and backwards along the floor of the lateral ventricles into the substance of the hippocampi, which are as largely developed as in the Wombat. The anterior part of the corpus callosum is bent downwards, and is attached along the middle line of its inferior surface by a uniting medium of medullary substance, representing the septum lucidum, to the hippocampal commissure or fornix. The tæniæ hippocampi, which form the lateral parts of this commissure, extend forwards, as in the Wombat, into the anterior lobes.

The corpus callosum being removed, and the commissural fibres of the hippocampi being left behind (as shown on the left side at Plate VI. fig. 5.), the view of the Beaver's brain now corresponds with that obtained in the previous dissection of the brain of the Wombat; which we regard, therefore, as wanting the corpus callosum, septum lucidum, and consequently the fifth ventricle. The artery of the plexus choroides, in both the Beaver and Wombat, enters the lateral ventricle, where the hippocampus commences at the base of the hemisphere, and the plexus is continued along the under surface of the tænia hippocampi, and passes beneath the fornix, through the usual foramen, to communicate with its fellow in the third ventricle, immediately behind the anterior crura of the fornix, which are sent down in the Beaver, as in the Wombat, from the centre of the inferior surface of the hippocampal commissure.

If we expose the lateral ventricle by removing its outer parietes in a marsupial and placental quadruped, as shown in Plate VII. figg. 4 and 5, in the Kangaroo and Ass, the hippocampus major (n), the tænia hippocampi (o), the plexus choroides (p), and the foramen Monroianum (γ) are brought into view. If a style be thrust transversely through the internal wall of the ventricle, immediately above the hippocampus, in the placental quadruped, it perforates the septum lucidum (q), and enters the opposite ventricle below the corpus callosum. If the same be done in the marsupial brain, the style passes into the opposite ventricle, but is immediately brought into view from above by divaricating the hemispheres, and is seen lying above the commissure of the hippocampi.

This commissure may nevertheless be regarded as representing, besides the fornix, the rudimental commencement of the corpus callosum; but this determination does not invalidate the fact that the great commissure which unites the supraventricular masses of the hemispheres in the Beaver and all other placentally developed Mammalia, and which exists in addition to the hippocampal commissure, is wanting in the brain of the Wombat: and as the same deficiency exists in the brain of the Great and Bush Kangaroos, the Vulpine Phalanger, the Ursine and Mauge's Dasyures, and the Virginian Opossum, it is most probably the characteristic of the marsupial division of Mammalia.

In the modification of the commissural apparatus above described, the Marsupialia present a structure of brain which is intermediate to that of the placental Mammalia and Birds, in which class the great commissure is wholly wanting, and the hemispheres, though comparatively larger than in many of the Mammalia, are brought into communication only by means of the anterior, posterior, and soft commissures, and a slight trace of the fornix or hippocampal commissure.

Of the other peculiarities of the marsupial brain, the relatively large size of the anterior commissure is most worthy of notice; its development is correspondent with the large size of the cerebral ganglion, which forms the chief origin of the olfactory nerve, and some of the anterior fibres arch forwards, and are directly continued into those nerves.

In the position, superficial transverse fissure, and solidity of the bigeminal bodies, the marsupial brain adheres to the mammiferous type, as also in the exterior transverse fibres of the commissure of the cerebellum, forming the pons Varolii, the presence of which is in relation with the development of the lateral lobes of the cerebellum.

Other minor points of difference between the brains of the Marsupiata themselves will be explained in the description of the figures.

Meanwhile their agreement in so important a modification of the cerebral organ as the absence of a corpus callosum and septum lucidum, affords additional and strong grounds for regarding the Marsupiata as a distinct and peculiar group of Mammalia; and when to this modification of cerebral structure are added the traces of the oviparous type of structure presented in the circulating and absorbent systems, together with the peculiarities of the osseous and generative apparatus, we may with reason suspect that distribution of the Marsupiata to be artificial and founded on an imperfect knowledge of their mutual affinities which, from a modification of the teeth and extremities alone, would separate and disperse the species amongst corresponding groups of the placental Mammalia.

Cuvier has observed that the marsupial group of quadrupeds embraces forms which typify different orders of the ordinary Mammalia*; and M. De Blainville regards them as forming, with the Monotremata, a division apart from the placental Mammalia. The metropolis of this subclass is the continent of Australasia, where the different carnivorous, insectivorous, omnivorous, and herbivorous genera act

* " Les Marsupiaux—nous paraissent devoir former un ordre à part, tant ils offrent de singularités dans leur économie, et surtout parceque l'on observe en quelque sorte la representation de trois ordres bien différents."—Règne Anim. i. p. 172.

corresponding parts to those performed by the placental Mammalia on a larger theatre, in which the avoidance of more numerous and powerful enemies, or the capture of more varied and subtle prey, demands the manifestation of more courage, the practice of more address, and the possession of more resources than appear to be called for by the exigencies of the Marsupiata in their more limited sphere.

Description of the PLATES.

PLATE V.

External form.

Fig 1. The upper surface of the brain of a Beaver (*Castor Fiber*, L.).
2. The upper surface of the brain of a Monkey (*Midas rufimanus*, GEOFF.).
3. The upper surface of the brain of a Wombat (*Phascolomys Wombatus*, BL.).
4. The upper surface of the brain of a Kangaroo (*Macropus major*, SHAW.).
5. The upper surface of the brain of an Ursine Dasyure (*Dasyurus ursinus*, GEOFF.).
6. The upper surface of the brain of a Virginian Opossum (*Didelphys Virginiana*, SHAW).
7. The base of the brain of a Beaver.
8. The base of the brain of a Wombat.
9. The base of the brain of a Virginian Opossum.

From these figures it will be seen that the convolution of the surface of the hemispheres of the brain does not take place in proportion as the hemispheres themselves are developed in superficial extent. They are fewer, for example, in the *Midas*, in which the hemispheres extend, as in most of the Quadrumana, over the greater part of the cerebellum, than in the Kangaroo or Wombat, where the cerebellum is left quite exposed. The brains of two species of herbivorous and two of carnivorous Marsupials are figured in this plate, to show indications of superior development which distinguish the brain of the herbivora, in the greater proportional development of the cerebrum, its convoluted surface, and the smaller proportional size of the olfactory tubercles. In all the species, but especially the carnivorous Marsupials, the greater relative size of the vermiform process is deserving of notice, as indicating the approach to the oviparous type of cerebral structure: it is associated with a corresponding diminution of the pons Varolii, as is strikingly shown in fig. 9.

PLATE VI.

Fig. 1. Side view of the brain of the Kangaroo.
2. Side view of the brain of the Virginian Opossum.

Structure.

Fig. 3. Brain of the Beaver, with the substance of the hemispheres removed to the level of the corpus callosum.

4. Brain of the Wombat, with the substance of the hemispheres removed to the level of the hippocampal commissure, except on the right side, where part of the thin internal wall of the lateral ventricle is left.

5. Brain of the Beaver, with the left cerebral hemisphere cut down to a level with the commissure of the hippocampus, and the lateral ventricle exposed. The corpus callosum has been vertically divided, and the left half removed, together with the hemisphere: the right hemisphere is entire.

6. A similar dissection of the brain of the Kangaroo, with the right hemisphere entire, and turned aside, showing the absence of the hemispheric commissure, corresponding to the corpus callosum of the Beaver.

The small size of the corpus striatum, *r*, as compared with the Wombat and Beaver, is shown in this view. The posterior bigeminal bodies are the broadest, the anterior the longest, in this animal as in the Beaver and Wombat.

PLATE VII.

Fig. 1. A vertical bisection of the brain of the Opossum (*Didelphys Virginiana*, SHAW), showing the large proportional size of the anterior commissure, *y*.

2. A vertical bisection of the brain of a Goose.

3. A lateral section of the left hemisphere, showing the lateral ventricle and hippocampus major in the Opossum.

The roof of the lateral ventricle is raised, showing it to be formed by fibres arching over the hippocampus, and continued from the inner margin of that part into those which radiate from the corpus striatum externally.

4. A similar dissection of the brain of the Kangaroo.

In this species the roof of the ventricle is proportionally thicker than in the carnivorous Opossum. Besides the diverging fibres of the crus cerebri, and those which pass in an arched form from the inner border of the hippocampus, over that body to the corpus striatum, there are others which form a thin layer, and pass into the tænia hippocampi, closely embracing the hippocampus: some of these are shown at *x x*.

The general disposition of the hemispheric fibres is such, that, supposing them contractile, they would draw the superficies of the hemisphere towards the crus cerebri, as to a fixed point, and compress the bodies projecting into the ventricles.

5. A similar dissection of the brain of the Ass. The dotted line shows the extent of the corpus callosum.

The same letters indicate the same parts in each figure.

A. Cerebral hemispheres.
B. Optic lobes, or corpora quadrigemina.
C. Cerebellum.
* Place between the vermiform process and lateral lobes, where the medullary matter of the cerebellum is superficial.
a. Olfactory lobes or ganglions.
b. Pons Varolii, or cerebellic commissure.
c. Corpus trapezoideum.
d. Corpora pyramidalia.
e. Crura cerebri.
f. Corpus albicans.
g. Infundibulum.
h. Pituitary gland.
1 *a*. Natiform protuberance, giving off the external root of the olfactory nerve.
1 *b*. Pyriform protuberance, forming the origin of the internal root of the olfactory nerve.
1 *c*. Medullary root of the olfactory nerve emerging from a longitudinal fissure in the natiform protuberance.
i. Fissure dividing the external root of olfactory nerve from the superincumbent hemisphere.
2. Chiasma of the optic nerves.
3. Third pair of nerves.
4. Fourth pair of nerves.
5. Fifth pair of nerves.
6. Sixth pair of nerves.
k. Corpus trapezoideum.
l. Corpus callosum, or commissure of the hemispheres.
m. Fornix, or commissure of the hippocampi.
n. Hippocampus major.
o. Tænia hippocampi.
o'. Anterior fibres of the tænia hippocampi continued into the anterior lobes of the hemispheres.
p. Plexus choroides.
q. Septum lucidum, or internal wall of the lateral ventricle (Plate VII. fig. 5.).
r. Corpus striatum.
s. Continuation of the lateral ventricle into the olfactory nerve.
t. Optic thalami.
u. Pineal gland.
x. Part of a thin stratum of medullary fibres arching over the hippocampus major, and continued into the internal wall of the ventricle.

y. The anterior commissure.
z. Soft commissure.
m. Hippocampal commissure.
α. The third ventricle.
β. The iter ad infundibulum.
γ. The foramen Monroianum.
δ. The iter ad quartum ventriculum.
ε. The valvula Vieussenii.
ζ. The fold of the valve corresponding to the posterior commissure.

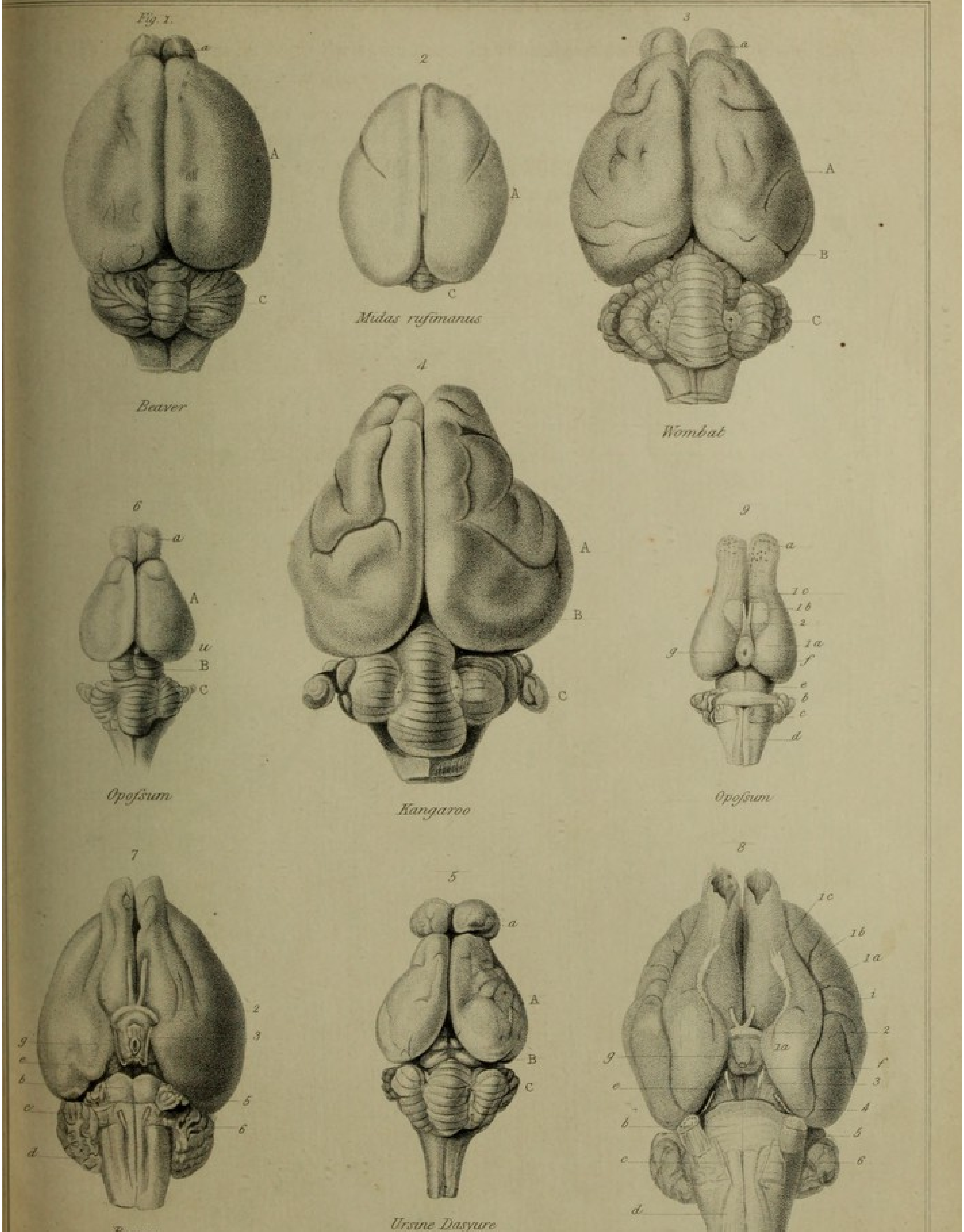

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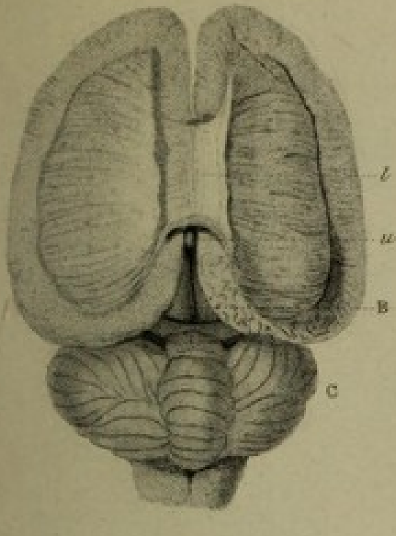
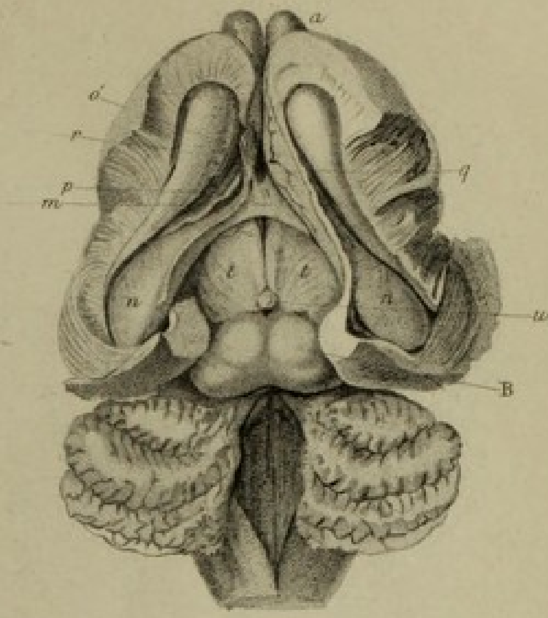
Fig. 3.



Beaver. No. 11.

Fig. 4.



Wombat. No. 12.

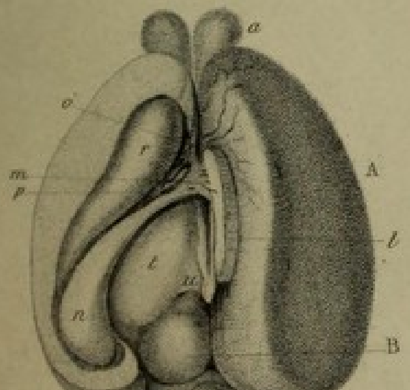
Fig. 1.

Kangaroo

Fig. 2.

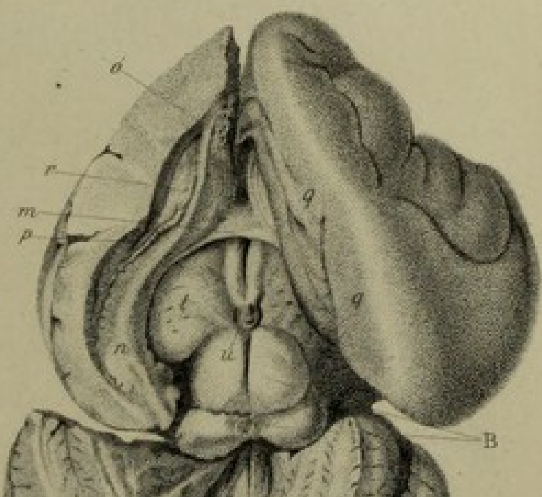
Opossum.

Fig. 5.



Beaver.

Fig. 6.



Kangaroo.

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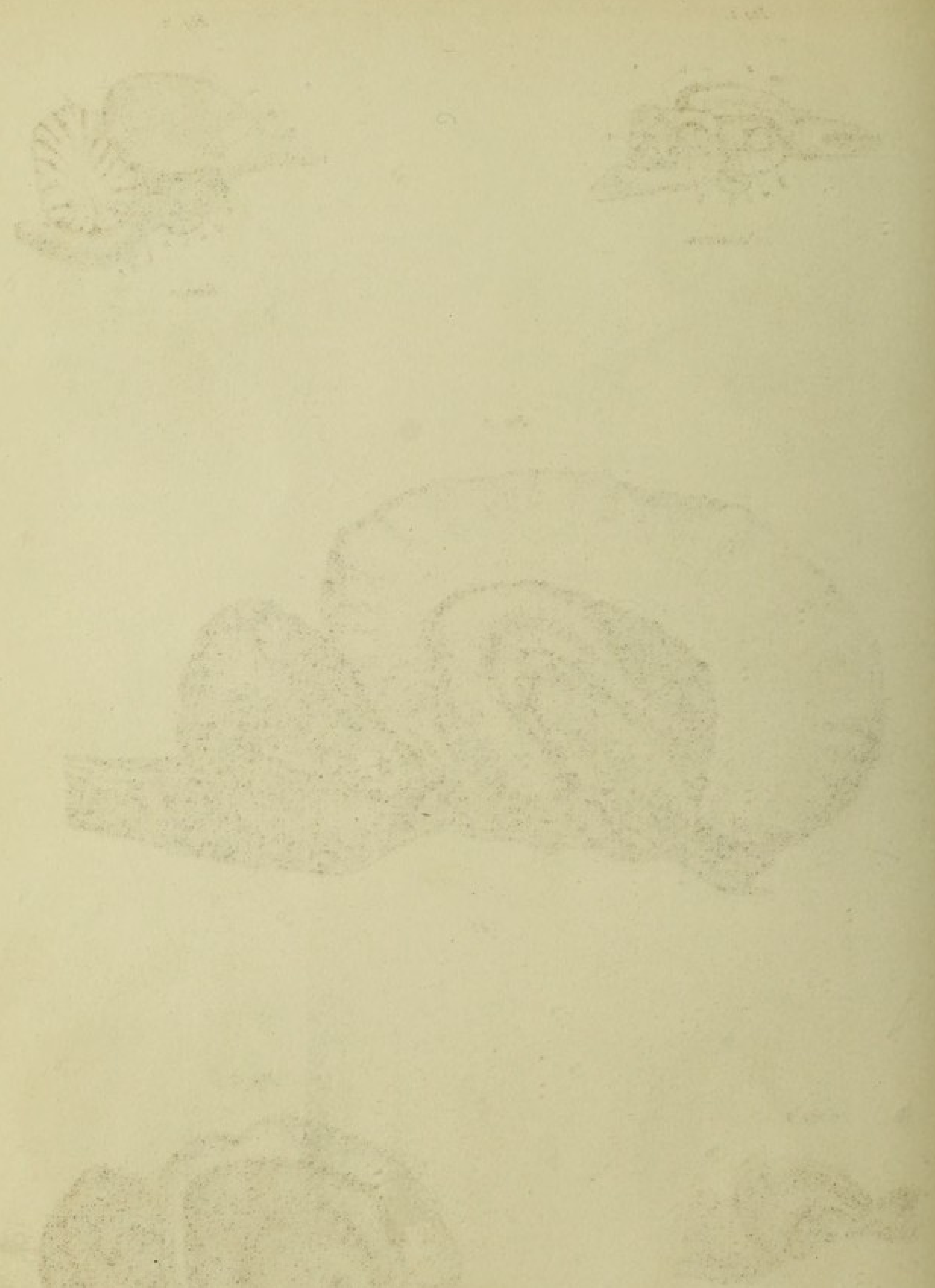
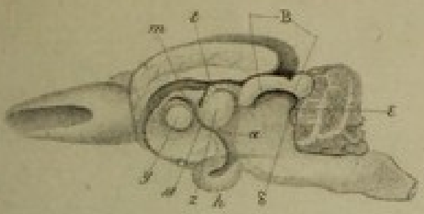
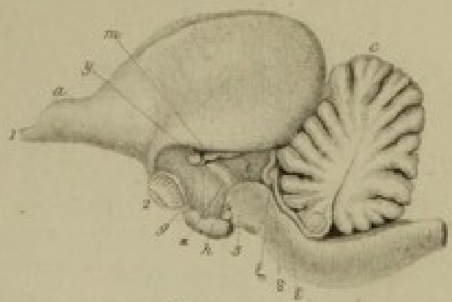


Fig. 1.



Opossum.

Fig. 2.



Goose.

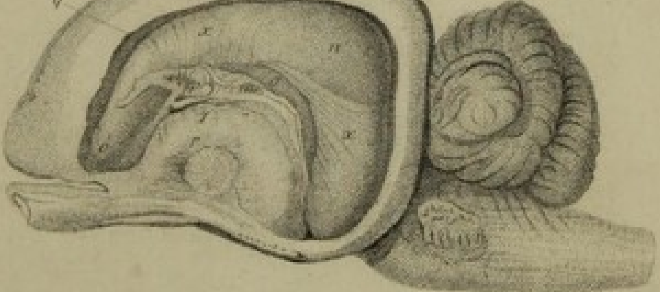
Fig. 5.

Ass.

Fig. 3.

Opofsum.

Fig. 4.



Kangaroo.

del.

J. Basire sc.