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The Intracranial Vascular System of Sphenodon

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X. *The Intracranial Vascular System of* Sphenodon.

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[Plate 31.]

In the course of my investigations on the Pineal Apparatus of the Tuatara (*Sphenodon punctatus*) I have found it desirable to make as complete a study as possible of the arrangement of the intracranial arteries and veins, of which no description has as yet been published. As any facts relating to the structure of *Sphenodon* are of more than usual interest, and as I hope to be able to give a more complete account of the subject than has yet been given for any reptile, I have decided to offer my results for publication as a separate memoir, without waiting for the completion of my work on the pineal organs.

The blood-vessels have been investigated partly by dissection and partly by means of serial sections, and such completeness of detail as I have been able to attain is very largely due to the adoption of a method of fixing and hardening which I have found to have many advantages both for the study of the vascular system and of the brain itself. By this method the entire contents of the cranial cavity are fixed and hardened *in situ*, and are then in excellent condition either for dissection or for histological purposes. The application of the method in the case of *Sphenodon* is greatly facilitated by the fact that the brain does not occupy nearly the whole of the cranial cavity, a large subdural space being left, especially above the brain, across which numerous blood-vessels run, together with delicate strands of connective tissue which connect the *dura mater* with the *pia*.

The animal is killed by chloroform, and the eyeballs are carefully removed from the orbits with as little loss of blood as possible. An incision is then made on each side in the cartilaginous wall which separates the cranial cavity from the orbit (at the point marked x in fig. 3, Plate 31). Through the incisions thus made the fixing fluid is gently injected into the cranial cavity by means of a pipette. The fluid used is acetic bichromate, made up according to the formula given by Bolles Lee, viz. :—

Bichromate of potash	3 grammes
Glacial acetic acid	5 c.c.
Water	100 c.c.

The entire animal, after opening up the body cavity, is then suspended in a large volume of the same fluid, which is changed after the first few hours. After about five days it is taken out and washed in running water for two or three hours, then slowly graded up through 15, 30, and 50 to 70 per cent. alcohol, which will probably have to be changed once or twice to complete the removal of the bichromate.

When the cranial cavity is now opened up, the cerebral blood-vessels are seen with extraordinary distinctness, although they have not been artificially injected. The greater part of the intracranial vascular system can thus be made out without any trouble, and the remainder may be investigated by means of sections. For this purpose it is possible to remove the greater part of the vessels with the brain and the *dura mater*, the latter supporting the vessels which run across the wide subdural space from the upper surface of the brain; but the great sinuses, lying in the *dura mater*, adhere closely to the cranial wall, and cannot be removed without injury. For the complete investigation of these and of the channels by which the blood leaves the cranial cavity, I have found it necessary to make use of serial sections through the cranium and its contents together. The difficulty of decalcifying so large an object, however, is a very serious drawback to this method, especially when it is desired to preserve the brain in a condition for minute histological work.

I have fortunately also been able to make use of sections of very advanced embryos of my Stage S, prepared by Prof. Howes and Mr. Swinnerton for their work on the development of the skeleton (1901) from material which I sent from New Zealand some years ago.

I have much pleasure in expressing my indebtedness to the Government Grant Committee of the Royal Society, which provided the necessary funds for obtaining a number of living Tuataras from New Zealand, primarily for my investigations on the pineal organs; to the Hon. W. Pember Reeves, late High Commissioner for the Dominion of New Zealand, and my old friend and colleague Prof. H. B. Kirk, of Wellington, New Zealand, without whose ready help it would hardly have been possible to obtain the specimens; to my pupil, Miss A. Hill, B.Sc., for assistance in tracing, by means of dissections, the connection of the intracranial vessels with those outside the cranium, and to my assistant, Mr. Charles Biddolph, for much valuable help in the preparation of the sections.

The Intracranial Arterial System.

The Internal Carotid Arteries (Plate 31, figs. 1, 2, 3, *a.c.i.*) enter the cranial cavity ventrally, one on either side of the infundibulum, and immediately below the foramen for the third nerve (fig. 3). Each divides as usual into two main portions, anterior (= *ramus cranialis* of Hofmann), and posterior (= *ramus caudalis* of Hofmann), which come off at right angles from the carotid, and lie practically in line with one another beneath the brain (figs. 1, 2).

The anterior divisions, right and left, pass forwards alongside the base of the infundibulum and the optic chiasma, beneath the cerebral hemispheres, and give off the following branches from behind forwards:—

1. *Arteriæ cerebrales posteriores* (figs. 1, 2, *a.c.p.*). A posterior cerebral artery comes off close to the point of division of the internal carotid and takes a somewhat sinuous course upwards between the optic lobe and the cerebral hemisphere. At about the level of the top of the optic lobe it divides into two branches, one, which I propose to term the saccular artery, running upwards alongside the dorsal sac, and the other, which I propose to term the superior cerebral, running forwards over the top of the cerebral hemisphere.

1*a*. *Arteriæ sacculares* (fig. 1, *a.s.*).—The saccular artery of each side runs upwards close alongside the wall of the dorsal sac and supplies the corresponding half of the choroid plexus of the dorsal sac. It also gives off branches to the wall of the pineal gland, especially (on one side) two important branches, the anterior and posterior pineal arteries. It is a remarkable fact that these branches may be given off from either the right or the left saccular artery.

1*a′*. *Arteria pinealis anterior* (fig. 1, *a.p.a.*).—This is an unpaired vessel which runs forward beneath the pineal gland (= "pineal stalk") and ultimately accompanies the pineal nerve to the pineal eye.

1*a″*. *Arteria pinealis posterior* (fig. 1, *a.p.p.*).—This runs backwards to the posterior portion of the pineal gland, lying at first between the wall of the pineal gland and the dorsal sac.

In one specimen the arrangement of the saccular arteries and their branches is as follows, as determined by a series of sections parallel to the sagittal plane. On the *right* side the saccular artery pursues an almost straight course upwards from its origin alongside the dorsal sac. When it reaches the upper limit of the latter, just beneath the opening of the right anterior choroidal vein into the longitudinal sinus (fig. 1), it becomes spirally twisted into a kind of knot, from which branches are given off on the inner side. Some of these branches supply the choroid plexus :* one, the posterior pineal artery, runs backwards and supplies the walls of the pineal gland, another smaller one runs more dorsally, while a very conspicuous branch, the anterior pineal artery, runs forwards beneath the pineal gland ("stalk"). The proximal portion of the anterior pineal artery is widely separated from the pineal nerve, which lies, as usual, on the left side, but I have no doubt it comes to lie close to the pineal nerve as it passes forwards, though, owing to these structures having been broken across when the brain was removed from the cranium for section cutting, this point could not be determined in this specimen. On the left side of the same specimen the saccular artery supplies the left half of the choroid plexus of the dorsal sac, but gives off no anterior pineal artery ; only a short branch, which divides into twigs supplying the walls of the pineal gland in the immediate neighbourhood, being present to represent both anterior and posterior branches of the opposite side.

In another specimen the *left* saccular artery gives off the anterior and posterior

* These are not shown in the figure.

pineal branches: the former (anterior pineal artery) running forwards beneath the pineal gland in close proximity to the anterior portion of the pineal nerve, while the latter can be traced backwards for some distance, also parallel with, but not so close

FIG. 1.

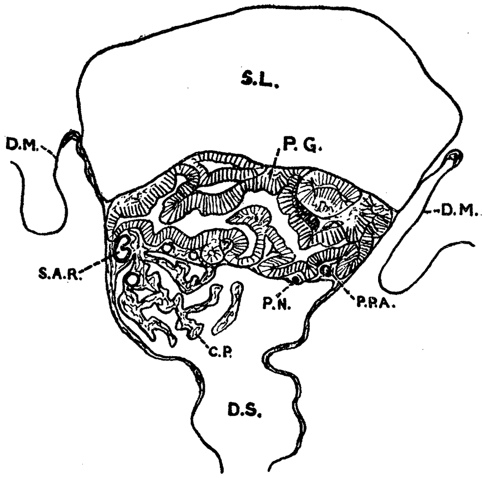

FIG. 2.

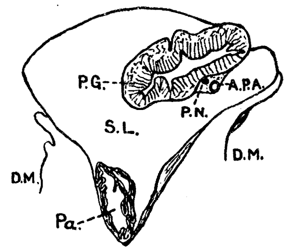

FIG. 1.—Section across the Sinus longitudinalis, Pineal Gland, and Dorsal Sac.

C.P., Choroid plexus of dorsal sac; D.M., Dura mater; D.S., Dorsal sac; P.G., Pineal gland; P.N., Pineal nerve; P.P.A., Posterior pineal artery; S.A.R., Upper portion of right saccular artery.

FIG. 2.—Section across the anterior part of the Pineal Gland (Pineal Stalk) almost completely surrounded by the Sinus longitudinalis, and across the upper part of the Paraphysis.

A.P.A., Anterior pineal artery; D.M., Dura mater; Pa., Upper part of the Paraphysis; P.G., Pineal gland; P.N., Pineal nerve; S.L., Sinus longitudinalis.

to, the middle portion of the pineal nerve; both lying, of course, on the left side. These relations were determined by means of a series of transverse sections (*vide* text-figs. 1 and 2).

1*b*. *Arteriæ cerebrales superiores* (fig. 1, *a.c.s.*).—The superior cerebral artery runs forwards over the top of the cerebral hemisphere, to which it gives off a number of twigs. Not far from the point where it leaves the saccular artery it gives off an important branch to the choroid plexus of the third and lateral ventricles.

1*b*′. *Arteriæ choroideæ anteriores* (fig. 1, *a.ch.a.*).—Each anterior choroidal artery enters the choroid plexus just in front of the *commissura aberrans*, along with the corresponding anterior choroidal vein. Thus the right and left anterior choroidal arteries lie side by side immediately in front of the commissure and immediately behind the right and left anterior choroidal veins.*

2. *Arteriæ infundibulares* (figs. 1, 2, *a.i.*).—An infundibular artery comes off on each side very slightly in front of the posterior cerebral. It is very short, passes inwards and downwards, and gives off twigs to the wall of the infundibulum.

* Both right and left anterior choroidal veins are shown in the diagram (fig. 1), but only the right anterior choroidal artery.

3. *Arteriæ cerebrales inferiores* (figs. 1, 2, *a.c.in.*).—An artery, which we may term the inferior cerebral, comes off beneath each cerebral hemisphere at a considerable distance in front of the infundibular artery and passes up into the fissure between the hemisphere and the optic tract, disappearing from view after a very short course. Sections show that it goes to the ventral surface of the posterior lobe of the hemisphere, in the neighbourhood of the *corpus striatum*, which it probably supplies.

4. *Arteriæ cerebrales mediæ* (figs. 1, 2, *a.c.m.*).—The middle, or "Sylvian," cerebral artery of each side comes off immediately in front of the preceding and passes on to the outer side of the hemisphere, near the middle of the latter. It gives off branches to the wall of the hemisphere and then pursues an undulatory course forwards to the olfactory stalk, forming the olfactory artery.

4*a*. *Arteriæ olfactoriæ* (figs. 1, 2, *a.olf.*).—The olfactory arteries run forwards beneath the olfactory veins, above and somewhat to the outside of the olfactory stalks.

5. *Arteriæ chiasmaticæ* (figs. 1, 2, *a.ch.*).—A very slender chiasmatic artery comes off at a short distance in front of the preceding and passes inwards and backwards to enter the brain in the angle between the hemisphere and the optic chiasma.

6. *Arteriæ cerebrales anteriores* (figs. 1, 2, *a.c.a.*).—The anterior cerebral artery of each side comes off quite close to the last named, and passes inwards and upwards, close alongside its fellow of the opposite side, between the two hemispheres and just in front of the optic chiasma. There appears to be no connection between the right and left anterior cerebral arteries, so that the circle of Willis is incomplete in front. The anterior cerebral artery divides into branches which lie in close proximity to the branches of the terminal vein, just in front of the *lamina terminalis*. It is possible that there may be some anastomosis between the branches of the right and left cerebral arteries, but I have not detected any. At any rate there is no obvious completion of the circle of Willis such as occurs in the tortoise (*cf.* BEDDARD, 1905).

7. *Arteriæ ophthalmicæ* (figs. 1, 2, 3, *a.oph.*).—After giving off the last named artery the anterior division of the internal carotid is continued directly forwards on either side as the ophthalmic artery. The two ophthalmic arteries approach one another in front of and above the optic nerves, and each passes out of the cranial cavity into the orbit in contact with the thick sheath of the nerve, as shown in fig. 3.

The posterior division of the internal carotid passes backwards on the inner side of the third nerve to join its fellow of the opposite side in the mid-ventral line just in front of the roots of the fifth pair of cranial nerves. The union of the two forms the basilar artery (figs. 1, 2, *a.bas.*), but before they unite they give off the following branches:—

8. *Arteriæ bigeminales* (figs. 1, 2, *a.b.*).—A large bigeminal artery comes off from the outer side of each posterior division of the internal carotid just in front of the

root of the third nerve, and passes upwards and backwards between the fourth nerve and the optic lobe. It gives off several important branches, which ramify over the surface of the optic lobe, and then passes onwards towards the top of the cerebellum, disappearing from view beneath the *torcular Herophili*. From beneath the torcular it gives off an important cerebellar artery, and is then continued onwards as the posterior choroidal artery.

8*a*. *Arteriæ cerebellares* (fig. 1, *a.c.*).—Each cerebellar artery arises from the bigeminal above and slightly in front of the upper margin of the cerebellum, and runs downwards, giving off branches to the anterior face of the cerebellum. (A few very small arterial twigs which enter the lower portion of the anterior face of the cerebellum probably come from the middle of the bigeminal artery near the root of the fourth nerve.)

8*b*. *Arteriæ choroideæ posteriores* (fig. 1, *a.ch.p.*).—The posterior choroidal artery of each side passes beneath the *saccus endolymphaticus* along the anterior part of the roof of the fourth ventricle. It runs in the thickness of the latter to the choroid plexus, lying on the outside of the great posterior choroidal vein (*cf.* text-fig. 3).

9. A very small artery comes off from the inner side of each posterior division of the internal carotid just opposite to the origin of the bigeminal artery, and goes to the base of the brain beneath the optic lobe, between the infundibulum and the root of the third nerve (figs. 1, 2, *a.x.*).

10. *Arteriæ medullares anteriores* (figs. 1, 2, *a.m.a.*).—A rather small anterior medullary artery comes off on each side in front of the junction of the two posterior divisions of the internal carotid, and passes outwards and backwards for a short distance on the ventral surface of the medulla. These vessels appear to correspond to what BEDDARD (1905) terms the "anterior cerebellar" arteries in Lacertilia; but if they supply blood to the cerebellum at all in *Sphenodon*, it must be very small in amount.

The single *basilar artery* (figs. 1, 2, *a.bas.*), formed by the union of the right and left posterior divisions of the internal carotid, now passes backwards in the middle line as far as the more anteriorly placed roots of the twelfth nerves. At the level of the seventh pair of nerves it gives off the posterior medullary arteries.

11. *Arteriæ medullares posteriores* (figs. 1, 2, *a.m.p.*).—These arteries pass outwards and slightly backwards on the under surface of the medulla. They evidently correspond to the "posterior cerebellar" arteries of BEDDARD's nomenclature, but I have no evidence that they supply anything but the medulla, and it seems highly improbable, in the case of *Sphenodon*, that they should send any branches to the cerebellum.

Posteriorly the basilar artery divides into right and left halves again, only to reunite once more, just behind the roots of the first pair of spinal nerves, in the median *inferior* or *anterior spinal artery* (fig. 2, *a.sp.i.*) (= *Tractus spinalis ventralis* of

HOFMANN). An elongated lozenge-shaped loop, or *circus arteriosus* (figs. 1, 2, *c.a.sp.*), is thus formed by the separation of the two halves of the basilar artery, and from the middle of each side of this loop comes off the artery of the first spinal nerve (figs. 1, 2, *a.sp.I.*).

Comparison of the Intracranial Arterial System of Sphenodon *with that of other Types.*

We owe our knowledge of the encephalic arteries of the Reptilia chiefly to the works of CORTI (1847), RATHKE (1856, 1857, 1866), HOFMANN (1900), and BEDDARD (1905), while BERTHA DE VRIESE (1905) has discussed the general arrangement and significance of these vessels throughout the vertebrate series. The researches of these investigators make it possible to institute comparisons with several other reptilian types.

BEDDARD (1905) has given a summary of the chief characters of the encephalic arterial system in the Lacertilia and Ophidia for purposes of comparison with those of other vertebrates. In the Lacertilia he enumerates eight characters which we may conveniently take as a basis for comparison with *Sphenodon*.

1. "The entrance of the vertebral arteries into the anterior spinal marks the end of the medulla oblongata." The "vertebral arteries" of BEDDARD being obviously the same as what I have termed the "arteries of the first spinal nerves" (following the nomenclature used by HOFMANN), *Sphenodon* agrees with the Lacertilia in this respect.

2. "The posterior cerebellar arteries are the only conspicuous arteries arising from the basilar; they arise at about the middle of the medulla oblongata and behind the sixth pair of cranial nerves; they are occasionally asymmetrical with each other." The "posterior cerebellar" arteries being identical with what I have termed the "posterior medullary," the only difference to be noted in this connection is the very slight one due to the fact that in *Sphenodon* the arteries in question arise just in front of the roots of the sixth nerves.

3. "The anterior bifurcation of the basilar is at a more or less acute angle according to its position; the slender anterior cerebellar arteries are invariably given off from the bifurcated basilar behind the point of origin of the third nerves; the two branches of the basilar produced by bifurcation may be inequisized." In *Sphenodon* the two branches of the basilar (= posterior divisions of the internal carotids) are of equal size and comparatively long. The "anterior cerebellar" (medullary) arteries come off about half way between the point of bifurcation and the root of the third nerve.

4. "The point of entrance of the carotids is not invariably the same; it is sometimes in front of and sometimes behind the third pair of nerves." In *Sphenodon* it is in front of the roots of the third pair of nerves.

5. "The artery on each side to the corpus bigeminum sends branches to the

cerebellum and to the cerebral hemispheres. It arises in front of the entrance of the carotids." The latter part of this statement is certainly true of some lizards, *e.g.*, *Psammosaurus griseus*, as figured by CORTI (1847), but BEDDARD himself states that in the skink *Eumeces algeriensis* the carotids join the circle of Willis in front of the artery supplying the *corpus bigeminum*. In *Sphenodon*, also, the bigeminal artery lies well behind the entrance of the carotid on each side, and each gives off an important cerebellar artery. If there is a branch to the cerebral hemisphere, however, it must be very small.

6. "In front of this artery is one which runs towards the optic chiasma." Judging from BEDDARD's description and figure (1905) of the encephalic arteries in *Tupinambis nigropunctatus*, this artery, which he says is "precisely like that of other Lacertilia," would seem to correspond to the branch of the posterior division of the internal carotid which I have numbered 9 in the case of *Sphenodon*, but in the latter it is far behind the optic chiasma. Moreover, CORTI (1847) figures the chiasmatic artery in *Psammosaurus griseus* as coming off opposite what he terms the "middle cerebral." In *Sphenodon* the chiasmatic artery comes off from the anterior division of the internal carotid further forward still, actually in front of the chiasma and just behind the anterior cerebral.

7. "There are three cerebral or hemispheral arteries: the posterior reaches each hemisphere just at its junction with the corpus bigeminum; the middle one is Sylvian in position; the anterior cerebral gives off the ophthalmic; there is no distinct completion of the circle of Willis anteriorly." The three cerebral arteries here referred to all occur in corresponding positions in *Sphenodon*. There is, however, an additional one of considerable size which comes off just behind the "Sylvian" artery, and which I have termed the "inferior cerebral." There is also in *Sphenodon* no distinct completion of the circle of Willis anteriorly, but one can hardly say that the anterior cerebral gives off the ophthalmic, the latter being a direct continuation of the anterior division of the internal carotid.

8. "There is no strongly marked asymmetry in the cerebral arterial system of the Lacertilia." This also is true of *Sphenodon* (with the exception of the pineal arteries).

On the whole it is obvious that the arrangement of the cerebral arteries in *Sphenodon* agrees very closely with the Lacertilian type, the points of difference being of no more importance than some of those which exist between different lizards. The fusion of the primitive right and left halves of the basilar artery, however, appears to be less complete, both in front and behind, than is usual in Lacertilia, and in this respect we have some approach to the condition described by BEDDARD (1905) in *Testudo vicina*, and by HOFMANN (1900) in *Testudo græca*, where the basilar artery is completely double. BEDDARD is inclined to regard the double condition of the basilar artery in *Testudo* as a divergence from the original condition, partly because it is found nowhere else* and partly because he thinks that

* *Cf.*, however, HOFMANN (1900).

the presence of a closed circle of Willis in *Testudo* is evidence of modification. We need not question the latter opinion, but it is quite possible that the arterial system of *Testudo* may at the same time be primitive in other respects, and the double condition of the basilar artery is just what we should expect in a primitive form, for it is generally believed that it was originally a paired structure.*

It is hardly necessary to enter into a detailed comparison of the cerebral arteries of *Sphenodon* with those of other reptilian groups. In the Ophidia the principal differences appear to lie in a strongly-marked asymmetry due to the greater size of the left carotid, and in the very marked completion of the circle of Willis anteriorly (BEDDARD, 1905).

The cerebral arteries in the Crocodile, as described by RATHKE (1866), though agreeing in general arrangement, exhibit so many differences in detail that it is hardly worth while to attempt any exact comparison.

The arrangement of the cerebral arteries in *Sphenodon* strongly supports the view that that animal is closely related to the Lacertilia, though it approaches the more primitive condition of the Chelonia as regards the basilar artery.

The Intracranial Venous System.

Considering the small size of the brain and in comparison with the corresponding structures (so far as known) in other reptiles, the intracranial venous system in *Sphenodon* exhibits a remarkably high degree of complexity. There is, as usual, a median *sinus longitudinalis* (fig. 1, *s.l.*) lying in the *dura mater* immediately beneath the cranial roof, and therefore separated by a wide subdural space from the greater part of the upper surface of the brain. Immediately in front of the cerebellum the longitudinal sinus receives right and left a pair of very wide transverse sinuses (fig. 1, *s.t.*), whereby it may be divided, for the purposes of description, into anterior and posterior portions. These are separated by a *torcular Herophili* (fig. 1, *t.h.*), as RATHKE (1866), on the analogy of human anatomy, has termed the junction of the longitudinal and transverse sinuses in the crocodile. The anterior portion of the longitudinal sinus receives numerous well-defined veins, chiefly from the dorsal surface of the brain, while the posterior portion divides into the right and left posterior cephalic veins (figs. 1, 3, *v.c.p.*). The transverse sinus receives blood from several veins, coming chiefly from the lower surface of the brain. The blood leaves the cranial cavity partly through the posterior cephalic veins, which pass out through the jugular foramina, and partly through the transverse sinuses, by way of a special aperture in the cranial wall above the trigeminal foramen, as will be described in due course.

Sinus longitudinalis (anterior division) (fig. 1, *s.l.*).—This commences in the *dura mater* a short distance in front of the parietal foramen, beneath which it forms an irregular loop around the end of the "pineal stalk" and the pineal nerve. For

* *Vide* HOFMANN (1900) and DE VRIESE (1905).

some little distance it practically surrounds the "pineal stalk" (pineal gland), receiving blood also from the paraphysis and from the choroid plexus of the dorsal sac (*cf.* text-fig. 2). Further back it lies on top of the pineal gland (text-fig. 1), whence it extends posteriorly to the *torcular Herophili*. The *sinus longitudinalis* is very wide, and its cavity is broken up to a very variable extent by strands or trabeculæ of connective tissue, which evidently correspond to the *Chordæ Willisii* of human anatomy. It receives blood from the following well-defined veins :—

1. *Venæ olfactoriæ* (fig. 1, *v.olf.*).—A pair of olfactory veins run backwards along and above the olfactory stalks and then curve upwards above the cerebral hemispheres to open into the *sinus longitudinalis* just in front of the paraphysis.

1*a*. *Venæ cerebrales inferiores* (figs. 1, 2, *v.c.i.*).—An inferior cerebral vein runs forwards along the under surface of each hemisphere, right and left of the middle line. It commences just in front of the optic chiasma and anteriorly passes up between the proximal portions of the two olfactory stalks to join the olfactory vein.

1*b*. *Venæ cerebrales superiores* (fig. 1, *v.c.s.*).—Several superior cerebral veins arise from the sides and roof of each cerebral hemisphere and pass upwards through the intervening space to join the corresponding olfactory vein. The most posterior of these veins opens close to the junction of the olfactory vein with the longitudinal sinus, perhaps directly into the latter.

2. *Venæ choroideæ anteriores* (fig. 1, *v.ch.a.*).—A pair of veins arise from the system of choroid plexuses of the third and lateral ventricles, and leave the brain immediately in front of the *commissura aberrans*, side by side with the anterior choroidal arteries. They run vertically upwards, close alongside the wall of the paraphysis, right and left, and open into the *sinus longitudinalis* at their dorsal extremities. They are in contact with the wall of the paraphysis for some distance, and probably receive blood from it. The left anterior choroidal vein, in its upper portion, is much larger than the right one, owing to the fact that it receives the *vena terminalis*.

2*a*. *Vena terminalis* (fig. 1, *v.t.*).—I propose this name for a large unpaired vessel which comes up from between the cerebral hemispheres immediately in front of the *lamina terminalis*, receiving a conspicuous branch* from the anterior commissure and several from a plexus of veins which lies between the two hemispheres in this region. It opens into the left anterior choroidal vein.

3. *Venæ parapineales* (fig. 1, *v.pp.*).—A pair of large veins which arise from the roof of the brain between the habenular commissure and the optic lobes, in the neighbourhood of the posterior commissure, and which pass, accompanied by two or three much slenderer veins, to the lower extremity of the pineal gland, just behind

* I have not been able to demonstrate the actual opening of this branch into the *Vena terminalis*, but it comes so close to the latter vessel as to leave but little doubt on the subject.

the dorsal sac. They then pass upwards, one on each side of the pineal gland, near its hinder margin, and open into the *sinus longitudinalis* just where the latter parts company with the pineal gland. These veins are in intimate contact with the walls of the pineal gland throughout the upper part of their course, in fact they lie beneath the investing *pia*, and no doubt convey venous blood from the hinder part of the pineal gland to the *sinus longitudinalis*.

4. *Venæ bigeminales superiores* (fig. 1, *v.b.s.*).—A group of large veins (five in the specimen investigated and figured) arising from between the optic lobes and passing up to open into the *sinus longitudinalis* close to one another and close to the parapineal veins. There appear to be two pairs of superior bigeminal veins just behind the pineal gland and an unpaired fifth one a little further back.

4*a*. *Vena interbigeminalis longitudinalis* (fig. 1, *v.i.l.*).—I propose this name for a rather large unpaired vein which lies deep down in the fissure between the optic lobes and immediately upon the roof of the *iter* in the middle line. It forms part of the plexus of veins which ramifies over the medial surfaces of the optic lobes, and from which the superior bigeminal veins arise. It discharges its blood into the longitudinal sinus through one or more of the latter. It can be traced backwards to a point just in front of the roots of the fourth pair of cranial nerves, and it seems probable that it receives one or more branches from the median region of the base of the cerebellum, though I have not definitely established this point.

Sinus longitudinalis (posterior division) = *Sinus occipitalis posterior*, Rathke (fig. 1, *s.o.p.*).—Behind the *torcular Herophili* the *sinus longitudinalis* is continued backwards for a short distance above and between the two *sacci endolymphatici* (text-figs. 3 and 4, S.O.) before dividing into the right and left posterior cephalic veins.

5. *Venæ cephalicæ posteriores* (= *venæ cerebrales posteriores*, auctorum (figs. 1, 3, *v.c.p.*).—Versluys (1898) has already adopted the name "cephalic" in preference to "cerebral" for these veins in lizards, and, as they have nothing to do with the cerebrum proper, it appears to me desirable to follow him in this respect. The posterior cephalic vein of each side in *Sphenodon* passes outwards, downwards, and backwards, above and behind the *ductus endolymphaticus*, to the jugular foramen, through which it leaves the cranial cavity just behind the auditory capsule, in company with the ninth, tenth, and eleventh cranial nerves (compare text-figs. 5 and 7, V.C.P.). It adheres closely to the inner surface of the cranial wall, and may easily be recognised in this position after the brain has been removed from the cranial cavity, lying just behind the projection of the auditory capsule (fig. 3, *v.c.p.*).

Although the *venæ cephalicæ posteriores* come very near to the *foramen magnum*, as shown in text-fig. 5, I have not been able to find any branch leaving the cranial cavity through the latter, although I have examined serial sections both of the

FIG. 3.

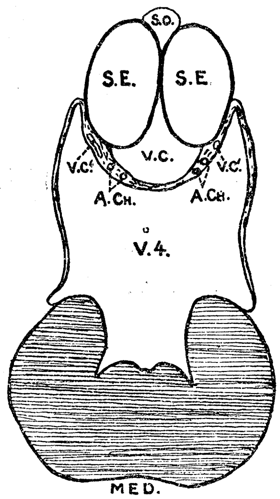

FIG. 4.

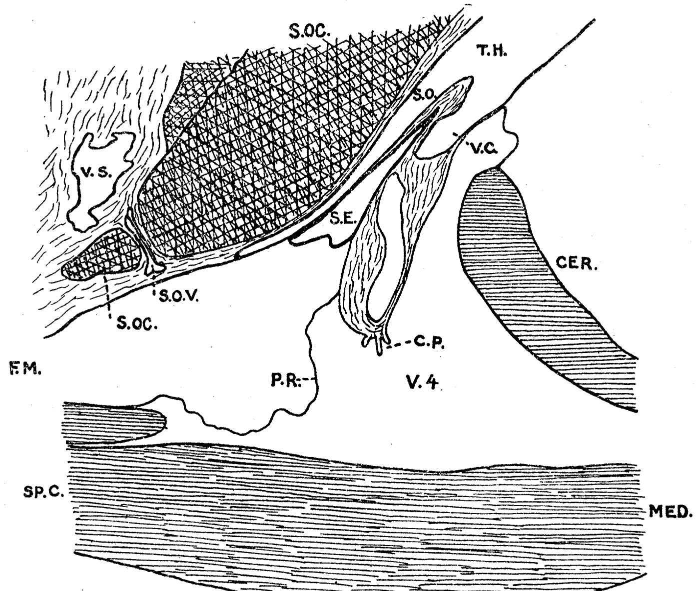

FIG. 3.—Section across the Fourth Ventricle, in front of the Choroid Plexus, and through the Sacci endolymphatici.

A.CH., Branches of Posterior Choroidal Artery; MED., Medulla oblongata; S.E., Saccus endolymphaticus; S.O., Posterior division of Sinus longitudinalis (Sinus occipitalis posterior); V.C., Great posterior choroidal vein; V.C.', Smaller posterior choroidal veins; V.4, Fourth ventricle.

FIG. 4.—Sagittal section (nearly median) through the Fourth Ventricle and Foramen magnum.

CER., Cerebellum; C.P., Choroid plexus of fourth ventricle (only a very small portion of this is visible, it is absent in the middle line); F.M., Foramen magnum; MED., Medulla oblongata; P.R., Roof of posterior portion of fourth ventricle; S.E., Saccus endolymphaticus; S.O., Posterior division of Sinus longitudinalis (Sinus occipitalis posterior); S.OC., Supra-occipital bone; S.O.V., Supra-occipital vein (the accompanying artery is also indicated); SP.C., Spinal cord; T.H., Torcular Herophili; V.C., Great posterior choroidal vein; V.S., Venous sinus; V.4, Fourth ventricle.

adult and of an advanced embryo (Stage S) with this end in view. There are a number of veins or sinuses in or about the occipito-atlantal membrane and above the supra-occipital bone (V.S. in text-fig. 5), and there is, at Stage S at any rate, a well-developed vein which passes down extracranially close to the ex-occipital bone, and probably communicates with the *vena cephalica posterior* (internal jugular) by a system of sinuses in the neighbourhood of the ganglion of the tenth nerve, but I have found no intracranial connection between the two. If there be one it must be extremely minute, and no blood worth speaking of can leave the cranial cavity through the *foramen magnum*, excepting of course that which passes out through the spinal veins.

My sagittal sections of the adult, however, show a very distinct median foramen in the supra-occipital bone, at a short distance in front of the *foramen magnum*. This foramen, which we may term the supra-occipital foramen, transmits a small vein and artery, as shown in text-fig. 4. The vein divides internally, in the *dura* *mater*, into two main branches, anterior and posterior. The anterior branch appears to be connected with the *sinus occipitalis*, or perhaps, more correctly speaking, with the upper part of the right *vena cephalica posterior*, but as I am not quite certain about this connection I have omitted it in the diagram (fig. 1). The posterior branch is less important and appears to come merely from the *dura mater*.

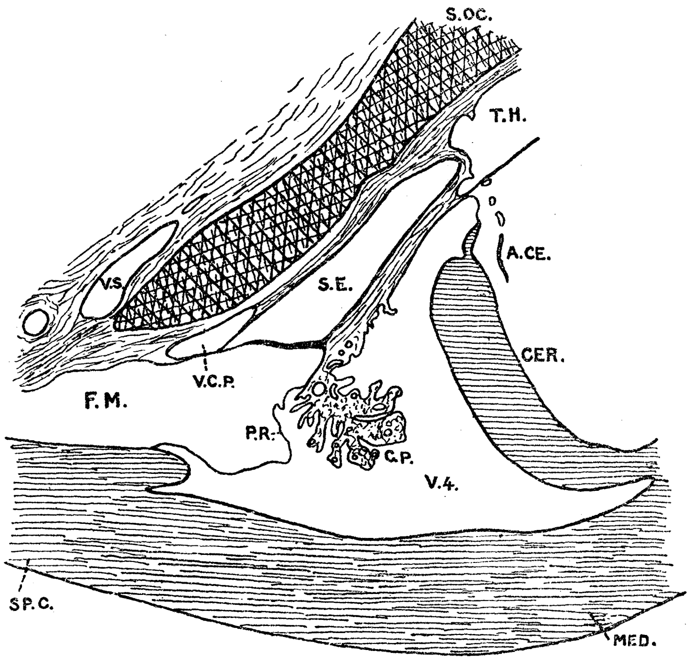

FIG. 5.—Longitudinal section through the Fourth Ventricle and Foramen magnum (from the same series as Fig. 4, but to one side of the middle line).

A.CE., Cerebellar Artery; CER., Cerebellum; C.P., Choroid plexus of fourth ventricle; F.M., Foramen magnum; MED., Medulla oblongata; P.R., Roof of posterior portion of fourth ventricle; S.E., Saccus endolymphaticus; S.OC., Supra-occipital bone; SP.C., Spinal cord; T.H., Torcular Herophili; V.C.P., Vena cephalica posterior; V.S., Venous sinus; V.4, Fourth ventricle.

Outside the cranium the vein lies close to a large venous sinus (V.S. in text-fig. 4), but I have not been able to trace its connections. As it passes through the foramen it receives a certain amount of blood from the supra-occipital bone, so that it may be regarded as in part a diploal vein. We may call it the *supra-occipital vein*.

The supra-occipital foramen is not present at stage S, but a well-marked sinus is present just behind the supra-occipital cartilage, and the foramen is probably formed by backward extension of the cartilage around this sinus or around a vein opening into it. I have also been unable to find the supra-ocipital foramen in the dry adult skull.

5*a*. *Venæ communicantes occipitales* (fig. 1, *v.c.o.*).—The posterior cephalic vein is connected with the *torcular Herophili* not only through the posterior division of the longitudinal sinus, but also by means of a vein which I propose to term the *vena communicans occipitalis*. This vein passes along the lateral and dorsal wall of the fourth ventricle, from a point just behind the *ductus endolymphaticus*, obliquely upwards and forwards to enter the torcular (or perhaps more strictly the proximal portion of the transverse sinus) immediately above the cerebellum. It receives small branches from the choroid plexus of the fourth ventricle.

5*b*. *Venæ spinales* (figs. 1, 2, *v.sp.*).—Just behind the point where the *vena communicans* is connected with the posterior cephalic vein the latter also receives a large *vena spinalis*, which runs forwards and upwards along the side of the medulla between the roots of the tenth cranial nerve. Traced backwards each spinal vein is seen to be a branch of a median ventral vein which lies beneath the spinal cord between the latter and the inferior spinal artery. As the inferior spinal artery divides, just behind the first spinal nerve, into right and left halves to form the *circus arteriosus spinalis* (figs. 1, 2, *c.a.sp.*), so the inferior spinal vein divides also into right and left branches. Each of these branches lies at first above the corresponding division of the inferior spinal artery (whereby it is concealed in fig. 2), but parts company with the latter just where the artery of the first spinal nerve is given off, and then continues its course forwards and upwards above the roots of the twelfth cranial nerve and between those of the tenth as already described.

A small vein from the choroid plexus of the fourth ventricle enters the posterior cephalic vein close alongside the spinal vein.

5*b*′. *Venæ medullares posteriores* (figs. 1, 2, *v.m.p.*).—Just behind the roots of the sixth nerve a vein arises by numerous branches from the ventral surface of the medulla on either side of the middle line. It runs backwards at first and then curves upwards and outwards to join the spinal vein just in front of the roots of the twelfth nerve.

Torcular Herophili (fig. 1, *t.h.*).—This name is applied to the wide sinus formed by the junction of the longitudinal and transverse sinuses, which may be regarded, for purposes of description, as extending laterally to the point of entrance of the *vena communicans* on each side. It receives the blood coming from the choroid plexuses of the fourth ventricle.

6. *Venæ choroideæ posteriores* (fig. 1, *v.ch.p.*).—In median sagittal sections the *sinus longitudinalis* (torcular portion) appears to divide above the cerebellum into a dorsal and a ventral portion (text-fig. 4). The former is, as we have already seen, simply the posterior division of the longitudinal sinus, or *sinus occipitalis*, which passes backwards *above* and between the *sacci endolymphatici* (text-fig. 3, S.O.). The latter, however, is much the wider of the two, and lies in the middle line on the roof of the fourth ventricle *beneath* and between the *sacci endolymphatici* (text-figs. 3 and

4,V.C.). It may be called the great posterior choroidal vein, and is made up by the union of a number of smaller veins coming right and left from the very largely developed choroid plexuses of the fourth ventricle. Other veins from these choroid plexuses enter the torcular more laterally, without joining the great choroidal vein, and others again, as we have already seen, enter the *venæ communicantes occipitales* and the posterior cephalic veins. The posterior choroidal vein is shown very diagrammatically in fig. 1.

Sinus transversi (= *venæ cerebrales mediæ* of GROSSER and BREZINA) (figs. 1, 3, 4, *s.t.*).—After the brain has been removed, the transverse sinus may be seen as a somewhat triangular, thin-walled sac lying against the wall of the cranial cavity, just in front of the prominence of the auditory capsule. In the specimen figured (fig. 3) the apex of the triangle, which lies dorsally, is truncated by its separation from the torcular, the longitudinal sinus having been removed with the brain, leaving a large aperture. The transverse sinus only extends about half-way down the cranial wall, so that it does not nearly reach the point of exit of the fifth nerve (fig. 3, V.); its lower margin, forming the base of the triangle, extends obliquely upwards and forwards from the auditory capsule. The outer wall of the sinus is closely adherent to the cranial wall, and indeed appears to be formed by the latter, which in this neighbourhood consists chiefly of dense connective tissue. The inner wall of the sinus is very thin, and is pierced by an aperture which lies not far from its lower margin and marks the point where the postgeminal vein has been detached (fig. 3, *op.v.pg.*). When the inner wall of the sinus is dissected off, and the blood washed out, a large slit-like opening is seen in the cranial wall, lying near the lower margin of the sinus (fig. 4, *op.s.t.*). Through this aperture a bristle can readily be passed into a vein which runs vertically downwards, outside the cranial wall and just in front of the auditory capsule, as far as the trigeminal foramen. This vein may be regarded as the extracranial portion of the *vena cephalica* (*cerebralis*) *media*. Probably a very large portion of the venous blood leaves the cranial cavity through this vein.

I have been able to verify my observations on the way in which the *sinus transversus* communicates with the extracranial portion of the *vena cephalica media* by means of serial sections of an advanced embryo of Stage S, a portion of one of which is represented in text-fig. 6. In this figure the *vena cephalica media* (V.C.M.) is seen passing downwards between the auditory capsule and the epipterygoid to the upper surface of the Gasserian ganglion. As the present memoir is concerned only with the intracranial veins, I have not followed its further course, but I have no doubt that it opens into the *vena capitis lateralis*, which SCHAUINSLAND (1900) has traced backwards in the embryo from about this point.

The slit-like opening by which the blood passes from the *sinus transversus* through the cranial wall is crossed, in the specimen examined and figured, by a stout band of connective tissue, which runs parallel with and a little above the lower margin of the opening, and lies close against the cranial wall, to which it is attached at its two ends, as shown in the figure (fig. 4). Above this opening and close to the antero-dorsal margin of the *sinus transversus*, lie two much smaller openings, one of which (fig. 4, *v.c.d.ap. ?*) is probably the opening of the *vena capitis dorsalis* into the *sinus transversus*.

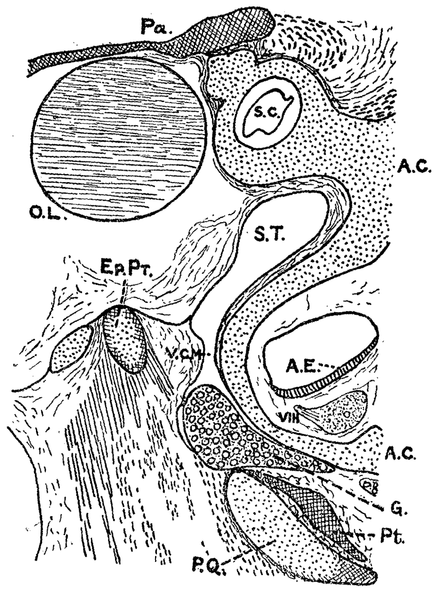

FIG. 6.—Vertical longitudinal section through the Point of Exit of the Vena Cephalica Media from the Cranial Cavity; from an advanced Embryo of Stage S. (Reversed as compared with figs. 4, 5 and 7.)
A.C., Auditory capsule; A.E., Auditory epithelium; EP.PT., Epipterygoid; G., Gasserian ganglion; O.L., Optic lobe; Pa., Parietal bone; P.Q., Pterygo-quadrate; Pt., Pterygoid; S.C., Semicircular canal; S.T., Sinus transversus; V.C.M., Vena cephalica media; VIII., Auditory nerve.
(Bone cross-hatched; cartilage dotted.)

The *vena capitis dorsalis* is not an intracranial vein, but comes from the muscles in the occipito-parietal region, and passes inwards just in front of the auditory capsule (text-fig. 7, V.C.D.). I have no doubt that it opens into the *sinus transversus* as described by BRUNER (1907) for *Lacerta*, where it "enters the cranium through the caudal end of the great parietal fissure" and joins the middle cephalic (cerebral) vein (= *sinus transversus*) close to the origin of the latter from the *sinus* (*vena*) *longitudinalis*. Unfortunately my sections are somewhat torn just where the actual opening into the *sinus transversus* should be, but the section represented in the text-figure is evidently taken just to one side of the opening.

7. *Venæ postgeminales* (figs. 1, 2, *v.pg.*).—As we have just seen, the *sinus transversus* of each side receives a large vein which returns blood chiefly from the ventral portions of the brain. Owing to its position behind the *corpora bigemina*, I propose to term this the postgeminal vein. The main trunk of the vein is short, but it is made up of several important branches.

7*a*. *Venæ subgeminales* (figs. 1, 2, *v.sg.*).—Commencing in the neighbourhood of the optic chiasma, and receiving small branches from the walls of the thalamencephalon, the subgeminal vein passes backwards beneath the optic lobe, from which it receives larger branches, to join the postgeminal.

7*a*′. *Venæ bigeminales inferiores* (fig. 1, *v.b.i.*).—This name may be applied to the important branches which the subgeminal vein receives from the optic lobe.

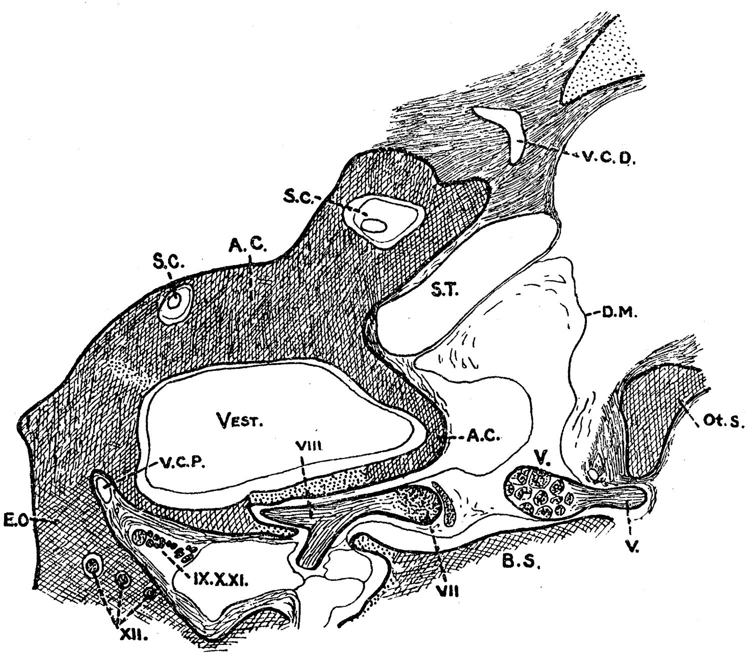

FIG. 7.—Vertical longitudinal section through the Auditory Capsule, Jugular Foramen, Sinus Transversus, etc.

A.C., Auditory capsule; B.S., Basisphenoid; D.M., Dura mater; E.O., Exoccipital; Ot.S., Otosphenoid; S.C., Semicircular canal: S.T., Sinus transversus; V.C.D., Vena capitis dorsalis; V.C.P., Vena cephalica posterior, lying in foramen jugulare; VEST., Vestibule of internal ear; V–XII, Cranial nerves.

(Bone cross-hatched; cartilage dotted.)

7*b*. *Venæ cerebellares* (fig. 1, *v.c.*).—The cerebellar vein of each side runs outwards, more or less transversely, across the anterior face of the cerebellum, from which it receives branches. It also receives an important branch from the side of the brain beneath the cerebellum and above the root of the fifth nerve, and a branch from the roof of the brain between the cerebellum and the optic lobe. It joins the postgeminal vein near the entrance of the subgeminal. In one case the cerebellar vein was observed to join the subgeminal just before the latter joined the anterior medullary to form the postgeminal.

7*c*. *Venæ medullares anteriores* (figs. 1, 2, *v.m.a.*).—The anterior medullary vein of each side arises from the under surface of the medulla by a number of branches which lie between the roots of the third and sixth nerves. It curves forwards and upwards alongside the brain in front of the trigeminal nerve and then curves backwards and becomes directly continuous with the postgeminal vein. Near its union with the subgeminal it receives an important branch from the side of the medulla in front of the fifth nerve.

Previous Observations on the Cephalic Veins of Sphenodon.

Scarcely any observations have hitherto been published on this subject. VERSLUYS, however, in his valuable work on the middle and outer ear of Lacertilia and Rhynchocephalia (1898), expressly states that no vein leaves the cranial cavity through the jugular foramen in *Sphenodon* (adult), though he concludes that all Sauropsida formerly possessed such a vein ("*Vena jugularis interna*"). GISI also (1907) was unable to find this vein in adult *Sphenodon*. SCHAUINSLAND, however (1900), described the existence in embryos of *Sphenodon* of an internal jugular vein accompanying the ninth, tenth, and eleventh cranial nerves through the jugular foramen, and further states that, in the embryo, the *vena lateralis capitis* runs parallel with and close to the main branch of the facial nerve, from the foramen of the latter dorsally and caudally, on the inner side of the facial artery, passing over the stapes and receiving the internal jugular (= *vena cephalica posterior*) coming from the *foramen jugulare*. It is obvious from my own observations and those of my pupil, Miss HILL, that the adult *Sphenodon* also possesses an "internal jugular" vein, which becomes continuous with the intracranial portion of the posterior cephalic vein at the jugular foramen.

Comparison of the Intracranial Venous System of Sphenodon *with that of other Types.*

Our knowledge of the intracranial veins of other reptiles is again very meagre. GROSSER and BREZINA (1895) have, however, laid the foundation for a comparative study of this question by their embryological investigations. From these researches we learn that the fundamental plan of the cephalic veins in its most primitive condition is as follows:—

On either side of the head, outside the brain case, runs the anterior part of the cardinal vein, longitudinally. This tends to be more or less replaced by a secondarily developed *vena capitis lateralis*. The most anterior portion of the jugular vein is formed from one or other of these vessels.

Inside the cranium, above the brain, runs a *vena longitudinalis cerebri*.* This is connected with the longitudinal veins outside the head primitively by three pairs of transverse vessels, the anterior, middle, and posterior *venæ cerebrales* (or better *cephalicæ*). The anterior pair run in the groove between the cerebral hemispheres and optic lobes, the middle pair between the optic lobes and the cerebellum, and the posterior pair at the sides of the medulla. The anterior pair seems always to

* = *Sinus longitudinalis* of this paper.

disappear in the adult. The fate of the middle and posterior pairs differs widely in different types.

Lacertilia.—In the lizard (*Lacerta*), according to GROSSER and BREZINA, only the posterior pair (*venæ cerebrales posteriores*) appear to persist in the adult, and these leave the cranium through the *foramen magnum* to join the jugular vein.

VERSLUYS also (1898) finds a posterior cephalic (= posterior cerebral) vein in many Lacertilia, and points out that it probably occurs in all. He further observes that nearly all *Lacertilia vera* possess an external jugular foramen which leads into the *recessus scalæ tympani,* and thence through the internal jugular foramen into the cranial cavity, and that CLASON (1871) maintained that he had followed a slender vein through this canal (in *Lacerta*) to the *vena lateralis capitis* (= *V. jugularis*, CLASON). VERSLUYS, however, could find no such vein in any of the Lacertilia investigated by him, with the exception of *Amphisbæna*, where it occurs in addition to the *vena cephalica posterior*, with which it unites outside the skull. GROSSER and BREZINA described a similar vein in embryos of *Lacerta*, but it disappears in the adult. VERSLUYS regards this vein as the homologue of the internal jugular of birds and mammals.

BRUNER (1907) again finds the posterior cephalic (cerebral) vein in *Lacerta* leaving the cranial cavity through the *foramen magnum*, and points out that it gives off the spinal vein, a matter of considerable interest as facilitating a comparison with *Sphenodon.* He also finds, however, in opposition to GROSSER and BREZINA, that the middle cephalic (cerebral) vein has in the adult a (secondary) connection with the jugular through the trigeminal foramen. He also finds a continuous *vena cephalica media* in *Agama.*

From these observations we may conclude that the Lacertilia differ from *Sphenodon* in that the posterior cephalic veins leave the cranial cavity through the *foramen magnum* and there is usually no vein passing out through the jugular foramen.

BRUNER also describes in *Lacerta* a *vena infundibuli* which I have not observed in *Sphenodon.* This is a median vein which lies on the posterior aspect of the infundibulum, and is formed by the union of right and left *venæ thalamencephali.* It divides into a pair of hypophysial veins which run around the hypophysis to the anterior end of the basisphenoid bone, where they enter the "*venæ cerebrales mediæ secundæ.*" In *Sphenodon* the blood from the wall of the thalamencephalon appears to be taken away by the subgeminal vein, but it is quite possible that there may also be a *vena infundibuli* as in *Lacerta.*

BRUNER'S brief account of the veins of the epiphysis in *Lacerta* differs widely from what I find in *Sphenodon.* He says: "The *venæ epiphyseos* have their roots in the cerebrum, where they drain the plexus chorioideus lateralis of the lateral ventricles. From each ventricle a single vein passes through the foramen Monroi and unites with its fellow in the roof of the third ventricle. The trunk vein ascends the stalk of the epiphysis, giving rise at the same time to a number of anastomosing branches, which form the plexus chorioideus anterior. From this plexus several small veins enter the ring of the vena longitudinalis cerebri."

A very large portion of the intracranial veins which I have found in *Sphenodon* appear to be still undescribed in Lacertilia.

Ophidia.—In the snakes the condition of the principal parts of the cephalic venous system appears to be essentially similar to that of Lacertilia.* BRUNER observes that the "*vena jugularis interna*" (= *vena capitis lateralis* of GROSSER and BREZINA) "runs directly caudad, following a course which lies close to the cranial wall and above the roots of the trigeminus and the more posterior cranial nerves . . . . Farther caudad it receives two large tributaries from the cranial cavity: the vena cerebralis media, which passes through the foramen for the second and third branches of the trigeminus, and the vena cerebralis posterior, which leaves the skull by way of the foramen magnum."

HASSE (*fide* VERSLUYS (1898)) has described a vein in *Tropidonotus* passing out through the jugular foramen, but VERSLUYS throws doubt on the existence of such a vein in snakes, and no such vein is mentioned by BRUNER (1907).

Chelonia.—With regard to this group, again, I take my information from BRUNER'S recent paper, which contains an account of the principal cephalic veins in *Emys europæa*. The general arrangement is again very similar to that of Lacertilia. The "*Vena jugularis interna*," corresponding to the *vena capitis lateralis*, together with part of the *vena cardinalis* of GROSSER and BREZINA, lies extracranially (not partly intracranially as stated by GROSSER and BREZINA), and receives a "*vena cerebralis media*," which leaves the cranial cavity through the trigeminal foramen, and a "*vena cerebralis posterior*." The condition of the latter is very interesting, for it leaves the cranium in two parts, one passing through the *foramen magnum* and the other through the *foramen jugulare*. In *Sphenodon*, as we have already seen, it leaves entirely through the *foramen jugulare*, and in Lacertilia usually entirely through the *foramen magnum*. Hence the Chelonia appear to occupy an intermediate position between *Sphenodon* and the *Lacertilia* in this respect. It is probably really in a more primitive condition, from which, by suppression of one or the other of the two branches, the condition of the Lacertilia has arisen on the one hand and that of *Sphenodon* on the other.

Crocodilia.—We learn from RATHKE'S work on the Crocodile (1866) that the wide *sinus longitudinalis* arises far forward in the cranial cavity by the union of *venæ nasales*, which probably correspond to what I have termed the *venæ olfactoriæ* in *Sphenodon*. At the boundary between the optic lobes and the cerebellum it forms a moderately large *torcular Herophili*, which gives off laterally a pair of *sinus transversi* and posteriorly a *sinus occipitalis posterior*. Near its lower extremity each transverse sinus receives a moderate-sized twig which runs backwards from the lower surface of one hemisphere of the cerebrum. Several smaller branches enter

* V. GROSSER and BREZINA (1895) and BRUNER (1907).

the *sinus transversi* and other branches enter the *sinus longitudinalis* from the upper side of the brain and the *dura mater*. So far this description agrees very well with what we find in *Sphenodon*, but RATHKE'S account of the manner in which the veins leave the cranial cavity is much more difficult to follow. He states that the two *sinus transversi* pass to the floor of the skull, where they enter the *foramina jugularia* behind the cerebral carotids, and at a considerable distance from the openings of the carotid canals. Unless there is some confusion here in the use of the term "*foramina jugularia*," this statement is quite inexplicable to me, but an illustration which the author gives (Plate 10, fig. 1) shows the *foramina jugularia* in the usual position at the sides of the *foramen magnum*. The *sinus transversus* of the crocodile is obviously homologous with that of *Sphenodon* and with the *venæ cerebrales (cephalicæ) mediæ* of reptiles generally, and it seems eminently improbable that they should enter the *foramina jugularia*. This point must await further investigation on the crocodile.

RATHKE also tells us that the "*vena jugularis interna*" enters the cranial cavity along with the vagus nerve, so that there appears to be no doubt that a vein does pass out through the jugular foramen. Another vein leaves the cranial cavity through the *foramen magnum* as in Lacertilia. This appears to come from the *sinus occipitalis posterior* by way of a bow-shaped venous plexus which RATHKE terms the *sinus foraminis magni*.

The *venæ spinales* are said to be connected anteriorly with the *sinus foraminis magni*, which perhaps indicates that the latter corresponds to the posterior cephalic (cerebral) veins of other reptiles.

RATHKE also describes a pair of blood-vessels corresponding in position to the *sinus cavernosi* of man and extending from the optic foramina to the internal carotid foramina. I have found no such vessels or sinuses in *Sphenodon*.

We may summarise the results of our comparison of the cerebral arteries and veins of *Sphenodon* with those of other reptiles as follows: On the whole the arrangement agrees with that of the Lacertilia, so far as these have been investigated, but there is an important difference in the fact that the *vena cephalica posterior* leaves the cranial cavity through the *foramen jugulare* and not through the *foramen magnum*, while a slightly more primitive condition is shown in the less completely united condition of the basilar artery. *Sphenodon* makes some approach to the condition of the *Chelonia* in this latter respect, but differs conspicuously from this group in the fact that the circle of Willis is not completed anteriorly, as well as in the fact that no branch of the posterior cephalic vein leaves the cranial cavity through the *foramen magnum*. A very characteristic feature of *Sphenodon* is the development of large transverse sinuses resembling those of the crocodile, but these communicate with the extracranial vascular system in quite a different manner from that described by RATHKE in the latter animal.

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DESCRIPTION OF PLATE.

a.b., Arteria bigeminalis; *a.bas.*, Arteria basilaris; *A.C.*, Auditory capsule; *a.c.*, Arteria cerebellaris; *a.c.a.*, Arteria cerebralis anterior; *a.ch.*, Arteria chiasmatica; *a.ch.a.*, Arteria choroidea anterior; *a.ch.p.*, Arteria choroidea posterior; *a.c.in.*, Arteria cerebralis inferior; *a.c.m.*, Arteria cerebralis media; *a.c.p.*, Arteria cerebralis posterior; *a.c.s.*, Arteria cerebralis superior; *a.i.*, Arteria infundibularis; *a.m.a.*, Arteria medullaris anterior; *a.m.p.*, Arteria medullaris posterior; *a.olf.*, Arteria olfactoria; *a.oph.*, Arteria ophthalmica; *a.p.a.*, Arteria pinealis anterior; *a.p.p.*, Arteria pinealis posterior; *a.s.*, Arteria saccularis; *A.Sp.I.*, First spinal artery; *a.sp.i.*, Arteria spinalis inferior; *a.x.*, Small unnamed artery; *Cart.*, Bridge of cartilage over meatus auditorius internus; *c.a.sp.*, Circus arteriosus spinalis; *Ce.*, Cerebellum; *C.H.*, Cerebral hemisphere; *c.p.A*, Choroid plexus of third and lateral ventricles; *c.p.B.*, Choroid plexus of dorsal sac; *c.p.C.*, Choroid plexus of fourth ventricle; *D.S.*, Dorsal sac; *e.o.*, Exoccipital bone; *f.j.*, Inner opening of foramen jugulare; *fr.*, Frontal bone; *Inf.*, Infundibulum; *i.o.s.*, Interorbital septum; *N.Sp.I.*, First spinal nerve; *o.a.m.*, Occipito-atlantal membrane; *O.Ch.*, Optic chiasma; *O.L.*, Optic lobe; *o.n.s.*, Sheath of optic nerve; *op.v.pg.*, Opening of postgeminal vein into sinus transversus; *Par.*, Paraphysis; *par.*, Parietal bone; *P.E.*, Pineal eye in its capsule; *P.G.*, Pineal gland; *Pit.*, Pituitary body; *P.P.*, Parietal plug; *s.l.*, Sinus longitudinalis; *s.o.*, Supra-occipital bone; *s.o.c.*, Supra-occipital cartilage; *s.o.p.*, Sinus occipitalis posterior; *s.t.*, Sinus transversus; *t.h.*, Torcular Herophili; *v.b.i.*, Venæ bigeminales inferiores; *v.b.s.*, Venæ bigeminales superiores; *v.c.*, Vena cerebellaris; *v.c.d.ap.* (?), Probable opening of vena capitis dorsalis into sinus transversus; *v.ch.a.*, Venæ choroideæ anteriores; *v.ch.p.*, Vena choroidea posterior; *v.c.i.*, Vena cerebralis inferior; *v.c.o.*, Vena communicans occipitalis; *v.c.p.*, Vena cephalica posterior; *v.c.s.*, Venæ cerebrales superiores; *v.i.l.*, Vena interbigeminalis longitudinalis; *v.m.a.*, Vena medullaris anterior; *v.m.p.*, Vena medullaris posterior; *v.olf.*, Vena olfactoria; *v.pg.*, Vena postgeminalis; *v.pp.*, Vena parapinealis; *v.sg.*, Vena subgeminalis; *v.sp.*, Vena spinalis; *v.t.*, Vena terminalis; *x.*, Point where incision is made in cranial wall for injection of cranial cavity; *II–XII*, Roots and foramina of cranial Nerves.

(Arteries coloured red, veins and sinuses blue.)

Fig. 1.—Diagram of cerebral veins and arteries of *Sphenodon punctatus*, side view. The sinus transversus and the lower part of the vena cephalica posterior are supposed to be removed. Vessels represented without outlines are supposed to be seen through overlying structures.

Fig. 2.—Diagram of cerebral veins and arteries of *Sphenodon punctatus*, ventral view.

FIG. 3.—Interior of cranial cavity of *Sphenodon punctatus*, after removal of the brain, left side. The unshaded areas on the inner surface of the cranial wall indicate the distribution of the dense white connective tissue of which the cranium is largely made up.

FIG. 4.—Interior of sinus transversus, showing the aperture in the cranial wall through which it communicates with the extracranial portion of the *vena cephalica media*.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

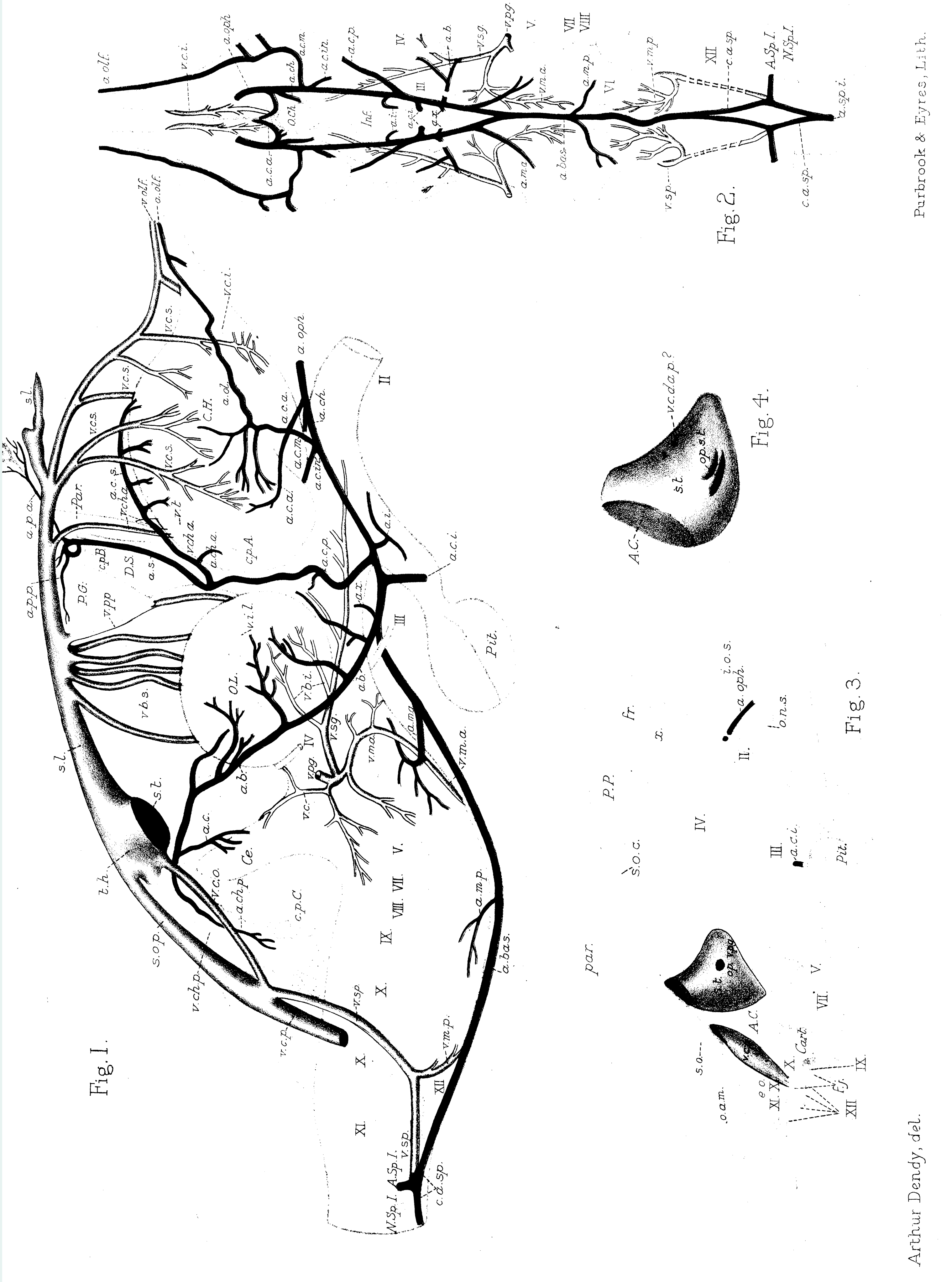
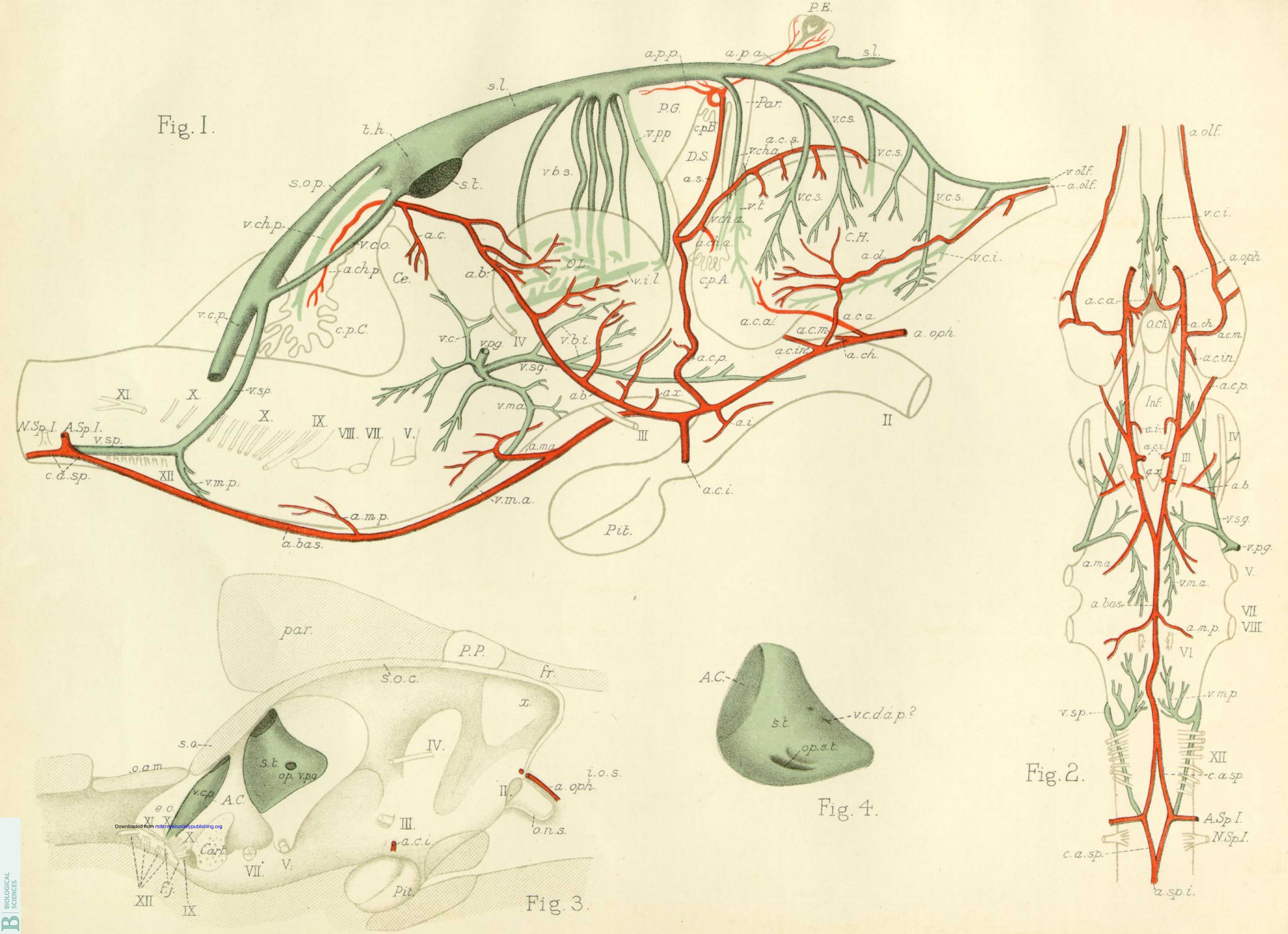


Fig. 1. Fig. 2. Fig. 3. Fig. 4.

Arthur Dendy, del.

Purbrook & Eyres, Lith.



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