VI.—*The Blood Vascular System of the Tuatara,* Sphenodon punctatus.

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[PLATES 6–8.]

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INTRODUCTION.

It is universally admitted that the Tuatara (*Sphenodon punctatus*) occupies a unique place among living Reptiles. By some authorities it is placed in the order Rhynchocephalia, of which it is the sole living representative; others, indeed, have suggested that it should be included in the order Lacertilia, but even in this case it

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is regarded as being one of the least specialised forms. It is, then, a primitive member of the class, and is now only to be found on certain islands off the coast of New Zealand, being so near to extinction that it has been placed under protection by the Government of that country. Any additions to our knowledge of the anatomy of this form therefore seem worthy of being placed on record, particularly when, as will be discussed later, they have some bearing upon its relationship with allied forms.

The animal is one of considerable importance, from the comparative point of view, and yet strangely enough no account of its blood vascular system as a whole has ever been given, either in general or in detail, nor is there, so far as I am aware, a satisfactory description of the general anatomy of the heart. Certain points concerning the arterial system have been described, but others have been left untouched, and the same may be said of the venous system. Indeed, in the case of the latter, although much comparative work has been done along certain lines, there is no good general account of the veins in any member of the order Lacertilia. This being so, it is hoped that the following pages, which contain a fairly full account of the blood vascular system in Sphenodon, will help to fill a noticeable gap in our knowledge of the circulatory system in the Reptilia. In conjunction with Prof. DENDY's account (22) of the intra-cranial vascular system in the same species, it furnishes a more complete account of the blood-vessels than is available even for any of the Lacertilia.

In 1908, Prof. DENDY, F.R.S., suggested to my then fellow-student at King's College, Miss A. W. HILL, B.Sc., that she should work out the vascular system of this important type, and this she proceeded to do. For this purpose, she injected several specimens, and made a number of dissections on the injected and on other uninjected examples. She also made a number of laboratory notes and a series of valuable drawings of her dissections. Before the work was completed, however, Miss HILL left the country, taking with her her notes and drawings. After some years, she found that she would not have an opportunity of completing the work, and Prof. DENDY, in view of the valuable nature and rarity of the material, asked me if I would finish it. This I gladly consented to do, and he placed the original specimens at my disposal. Miss HILL also very generously handed over to me all the notes and drawings she had made, and these, together with the dissections she had left, rendered my task much easier. The drawings have been particularly useful, and I have not hesitated to make full use of them, although in all cases where I have used them I have redrawn them with slight alterations, and this has been indicated by appending thereto both our initials. My own observations were made upon the actual specimens, and the laboratory notes like the drawings served as useful checks.

MATERIAL.

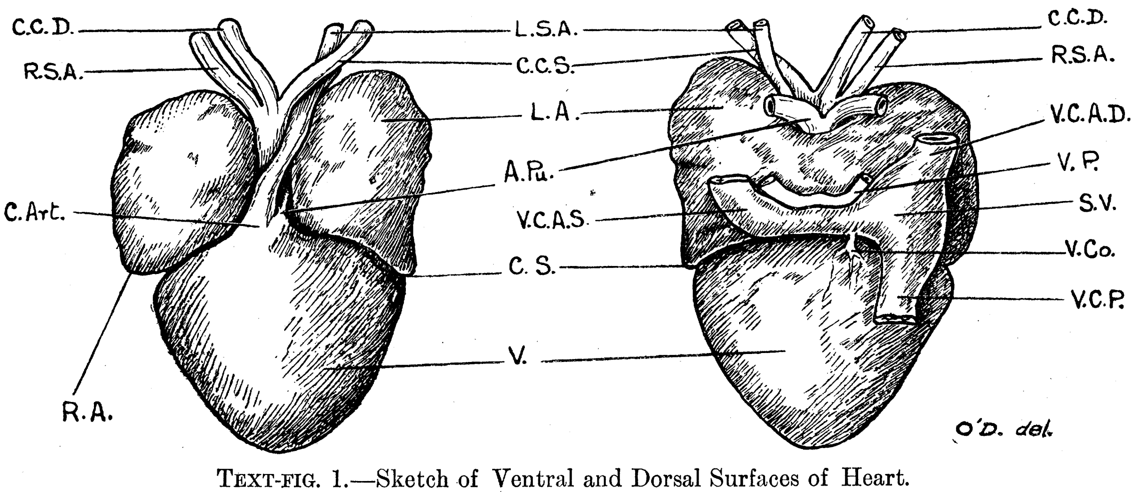
The material upon which these observations are based is a series of well preserved specimens of *Sphenodon punctatus* in the possession of Prof. DENDY, who had used them for his investigations on the intra-cranial vessels (*vide supra*) and on the Pineal apparatus and associated parts of the brain (23). They had been but little touched since they were left, and as they had been carefully preserved, I was enabled to make out practically all the details of the blood vascular system with the exception of one or two unimportant points which are referred to in their appropriate places in the text.

The brains of the injected specimens had been utilised previously, and so, in order to make out accurately the relations of the vessels, particularly the veins of this region, reference was made to series of transverse and longitudinal sections of the heads of late embryos used by Howes and Swinnerton in their investigation of the development of the skull (48). They were designated stages R and R–S, and are now in the possession of Prof. Dendy. In this connection I have to thank my former colleague, Dr. K. M. Parker, of University College, for helping me to make graphical reconstructions of the main vessels of these two stages.

My sincere thanks are due, firstly, to Prof. Dendy for affording me an opportunity of examining such an interesting and valuable species; and, secondly, to Miss A. W. Hill for unreservedly placing in my hands notes and drawings made from dissections which, as I well know, took a great deal of time and exhibited no little skill. Every advantage was taken of this work of Miss Hill, and I am conscious that some of the results set forth below would not have been possible without it.

The Heart (text-fig. 1).

In outward appearance the heart of *Sphenodon* is typically reptilian; it is not so elongated as in the Ophidia and many of the Lacertilia, nor so broad as in the



Text-fig. 1.—Sketch of Ventral and Dorsal Surfaces of Heart.

A.Pu., arteria pulmonalis; *C.Art.*, conus arteriosus; *C.C.D.*, carotis communis dextra; *C.C.S.*, carotis communis sinistra; *C.S.*, coronary sulcus; *L.A.*, left atrium; *R.S.A.*, right systemic arch; *S.V.*, sinus venosus; *V.*, ventricle; *V.C.A.D.*, vena cava anterior dextra; *V.C.A.S.*, vena cava anterior sinistra; *V.Co.*, vena coronaria; *V.C.P.*, vena cava posterior; *V.P.*, vena pulmonalis.

Crocodilia. It is about 28 mm. long in an average specimen, and when fairly well distended the atria measure about 30 mm. across. It lies, as in other forms, well forward in the pleuro-peritoneal cavity, practically in the median plane and between the lungs.

Sinus Venosus.—The sinus venosus is a well-marked thin-walled sac lying on the dorsal side of the heart just in front of the ventricle; it runs transversely, and the larger part of it is on the right side. It appears to be formed mainly by the confluence of the right anterior caval and the post-caval veins, and their openings are not separated by a semi-lunar ridge, the tuberculum intervenosum, such as we find in the Mammalia. Just to the left of the post-caval vein the coronary vein enters the sinus; it appears as a small but tough cord passing from the sinus across the coronary sulcus on to the wall of the ventricle, as in reptiles generally. To the left of this again, practically in the middle line of the heart, the left anterior caval vein enters the sinus. Outwardly it almost looks as if it were opening into the right atrium, but on slitting the wall of the sinus it will be seen opening into that structure. The aperture leading from the sinus to the atrium is guarded by two distinct valves about 5 mm. long and quite as well developed as in the Amphibia. These sinu-atrial valves lie in the median dorsal wall of the atrium, and run outwards and forwards at an angle of about 75 to the antero-posterior axis of the heart.

Atrium Dextrum.—The right atrium is actually larger than the left, but, as it does not pass so far caudally as the latter, it looks somewhat smaller when seen from the ventral surface. From its antero-dorsal edge near the middle line it gives off a small sac-like diverticulum with thin walls, and in two specimens in which the atria were distended with blood, this showed above the diverging bases of the Carotid arteries. It would appear, therefore, as if it was a normal structure, but its function is not obvious. Two portions of the atrium may be distinguished, the main cavity with thin walls and situated mesially and a postero-lateral auricle (auricula cordis) whose walls are thicker and marked internally by interlacing muscular ridges, the musculi pectinati. The two divisions, however, are not sharply defined and merge into one another more gradually than in the mammal.

Atrium Sinistrum.—The left atrium is on the whole very similar to the right in general structure and appearance. It is slightly smaller in size and the auricle at its postero-lateral corner overlaps the ventricle more than does the right. The two pulmonary veins open into its postero-mesial walls by a common aperture, which, while not guarded by a definite valve, is partly hidden by a fold of the atrial wall which may function as such.

The two atria from the outside seem to form a single sac, but internally they are completely separated by the septum atriorum. The septum, although slightly thinner in its central region, does not exhibit a distinct fossa ovalis such as we find in the Mammalia.

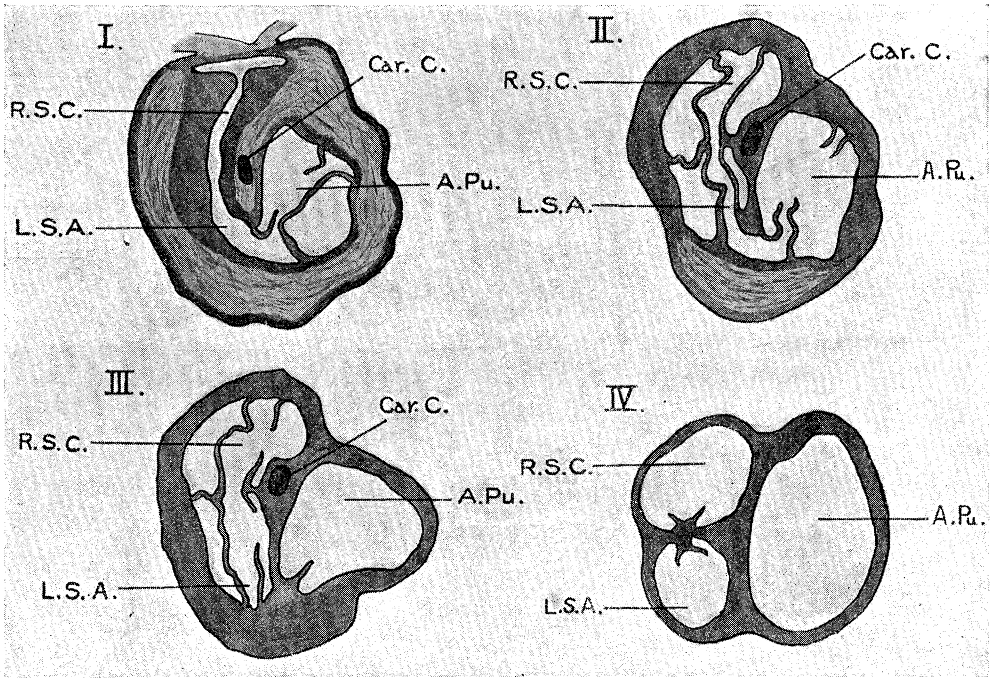
Ventriculus.—The ventricle is a stout-walled sac presenting somewhat the shape of an equilateral triangle when viewed from the ventral surface, and it is about 18 mm. long. It is sharply marked off from the atria by a well-developed coronary sulcus. Its apex is very bluntly rounded, and in one of the specimens examined bore short processes resembling the gubernaculum cordis that BEDDARD has stated to be present generally in the Lacertilia (3). The base of the ventricle is not quite at right angles to the long axis of the heart owing to the fact that the right shoulder is far more rounded off than the left. On the other hand, however, the left auricle overhangs the ventricle more than the right. The dorsal wall of the ventricle is more flattened than the ventral.

The arterial trunks come off slightly to the right of the middle line from a small anterior projection of the ventricle which, I think, is to be regarded as a remnant of the conus arteriosus for, although it does not bear characteristic conus valves, it nevertheless has valves and constitutes a sort of common trunk from which the arteries arise.

The lumen of the ventricle is quite small owing to the thickness of the wall, which is spongy and composed of an interlacing network of muscular trabeculæ into the interstices of which the blood can penetrate for a considerable distance. The two atria communicate with the ventricle by a common atrio-ventricular aperture situated on the dorsal side of the ventricle at its anterior end. They remain partially separated by an extension of the inter-atrial septum up to the opening which is guarded by a relatively thick flap that separates it from the base of the arterial opening, but does not appear to form a very definite valve. However, the state of preservation of the interior of the heart makes it difficult to speak with certainty on this point.

According to GOODRICH (36A) a small but distinct muscular septum ventriculorum is present in *Sphenodon*. A similar statement is made by GREIL (37), although in neither case is it figured or described in detail. This is a point on which I can make no definite statement as the preservation of the inside of the heart was not good enough to settle the point satisfactorily.

Trunci Arteriosi (text-figs. 1 and 2).—The arterial trunks, as has been noted, come off from a slight projection of the ventricle which is probably to be regarded as a remnant of the conus arteriosus. The three trunks, each guarded by a pair of deep semi-lunar valves, present certain points of interest. Viewed externally there appear to be three vessels from the commencement. These are the left systemic trunk, lying ventrally to the right, a right systemico-carotid trunk (*i.e.*, the vessel from which arise the right systemic arch and the two common carotids), lying dorsally and slightly to the right and the pulmonary arch, lying to the left side somewhat dorsally but just visible at the base of the ventricle from the ventral side. A reconstruction revealed the fact that the internal separation of the trunks was not complete, a point that was afterwards verified by careful dissection. At the base the three vessels stand in open communication with one another and pass backwards a short distance before their common lumen opens into that of the ventricle, and behind this again lies the atrio-ventricular aperture. This is, I think, the portion to be looked upon as the remnant of the conus arteriosus, and although only short is nevertheless quite distinct, and as it bears at its base one pair of semi-lunar valves obviously cannot be considered as part of the ventricle.



TEXT-FIG. 2.—Outline sketches of four sections through the Main Arterial Trunks, drawn with a Zeiss Meyer camera lucida and stand.

I. At the level where all three arterial trunks are in open communication and posterior to the valves of the right systemico-carotid and left systemic trunks (slide 14, No. 5).

II. At the level where all three trunks are still in communication but the valves in right systemico-carotid and left systemic trunks are fully developed (slide 17, No. 1).

III. At level where main septum completely separates the pulmonary artery but the right systemico-carotid and left systemic are in communication (slide 19, No. 8).

IV. At level where all three trunks are completely separated; at front limit of valves and anterior to the cardiac cartilage (slide 22, No. 10).

A.Pu., arteria pulmonalis; *Car.C.*, cardiac cartilage; *L.S.A.*, left systemic arch; *R.S.C.*, right systemico-carotid.

THE ARTERIAL SYSTEM.

The groundwork of our modern knowledge of the arterial system in the Saurians was laid by CORTI, in 1847, in his detailed account, 'De Systemate Vasorum *Psammosauri Grisei*,' in which he also gives a short account of previous work. This was followed ten years later by a splendid paper by RATHKE (66), dealing with the aortic roots in general and based upon an examination of 55 different species of Lacertilia and Crocodilia. He did not, however, examine *Sphenodon*. Since this time considerable additions to our comparative knowledge of various parts of the system have been made. In the first place, RATHKE (67) and HOCHSTETTER (44) have described the main gut arteries in many species. Secondly, ZUCKERKANDL (82, 83, and 84) has treated the arteries of the fore and hind limbs in a series of Amniotes, including Lacertilians; and, thirdly, BEDDARD (3, 4, 5, and 7) has investigated the relationship of various arteries in a number of different forms.

As far as *Sphenodon* itself is concerned, it has only been very incompletely studied. VAN BEMMELEN (10), in 1887, wrote a description of the neck region, in which, although mainly concerned with the nerves and their primitive relations to the branchial arches, certain of the neck arteries are accurately described. The main limb arteries were examined by ZUCKERKANDL (*loc. cit.*), and BEDDARD (7) dealt with the main arteries coming from the anterior part of the dorsal aorta. The visceral arteries were first treated, but in a very brief manner, by KLAATSCH (50), and this work was later extended by HOCHSTETTER (44). Finally, DENDY (22), from the same specimens he placed at my disposal, described in detail the intra-cranial arteries, which are therefore omitted here, save that their connections with the extra-cranial vessels are pointed out.

The presence of semilunar valves at the bases of the three arterial trunks and the points of origin of these vessels have already been dealt with. They pass forward together on the ventral side between the median walls of the atria, rotating slowly in a clockwise direction as they do so. Thus, the left systemic trunk starts from the conus ventrally and to the right of the group, and leaves the anterior end of the heart on the left side dorsal to the carotid arch. The pulmonary trunk commences on the left side and leaves dorsally; the right systemico-carotid trunk arises on the right dorsal and finishes on the right ventral side. Thus it will be seen that, while there is a certain amount of twisting, it is not as great as in other Reptiles.

The arterial system is best dealt with by describing the course and distribution of the three arterial arches arising from the three trunks, starting with the anterior pair.

The Carotid Arch (Plate 7, figs. 2 and 3).

The two common carotid arteries take origin together practically in the middle line, from the same point on the right systemic arch just as it commences to bend outwards over the trachea. There is thus no joint trunk or carotis primaria for these two vessels.

According to RATHKE (66, p. 62), two different arrangements are met with in the Lacertilia; in the one the two common carotids come off separately from the right systemic arch, and in the other they come off from a common carotis primaria, which in its turn arises from the right systemic. Even when present, the carotis primaria varies considerably in development, reaching its maximum in the *Varanidæ*, where it is quite long, and becoming so small in certain groups, including the *Lacertidæ*, that it may readily be overlooked. The two vessels in *Sphenodon* certainly have one common opening into the right systemic arch, but they do not run together until this point, and so it is not possible to speak of a carotis primaria in this form. It is difficult to say whether this approximation to the condition of the *Lacertidæ* is indicative of phylogenetic relationship. The point in itself cannot be pressed too far, as a similar range of differences occurs in the Ophidia ; in *Boa*, for example, the two common carotids come off separately, while in *Tropidonotus* a well-developed carotis primaria is present (58).

The two common carotids and their branches in *Sphenodon* pursue almost identical courses on the two sides of the neck and head, save perhaps in some of their smaller unimportant twigs, so that the description given for one side will apply equally well to the other.

The Carotis Communis (RATHKE, CORTI) (Plate 7, figs. 2 and 3, text-figs. 6 and 7).—The common carotid runs sharply outwards and slightly forwards round the trachea to the latero-ventral wall of the œsophagus, where it divides into two branches, the external carotid (B) and the internal carotid (C). Close to its origin it gives off a small vessel (A). RATHKE has noticed three different conditions of the common carotid in the Lacertilia in general : (1) In the *Varanidæ*, where the heart lies a long way back from the head, not only is a carotis primaria developed, but the common carotid runs a good way up the neck before dividing into external and internal branches. A ductus caroticus joining the carotid to the systemic arch is not present. (2) Similarly in the *Chamæleontidæ* no ductus caroticus is present save in *Chamæleon planiceps*, where it is still to be found on each side as a very fine vessel visible only with a hand lens. (3) The third group includes most of the remaining forms where the heart, as a general rule, is not far back from the head, and in these a ductus caroticus is present. The condition in *Sphenodon* is very similar to that in the *Lacertidæ*.

A. *Arteria pericardialis* ('Arterie für das Pericard.,' v. BEMMELEN (10)) is a small vessel going to the pericardium.

B. *Carotis externa* (v. BEMMELEN ; Ramus trachealicus, CORTI ; 'Kehl-Zungenast des Carotidenbogens,' RATHKE) (Plate 7, fig. 3, text-fig. 7).—The external carotid is a fairly small artery arising from the outer wall of the common carotid, and it runs forward close to the œsophageal wall and gradually outwards, keeping laterad of most of the nerves of the neck. It is a continuation forward of the ventral aorta of the embryo. With the exception of a small thyroid branch (B. I), it remains a single trunk up to the hyoid region. Just after crossing the outer surface of the ceratohyal it is itself crossed ventrally by the hyo-maxillary branch of the twelfth cranial nerve, the largest nerve in this region, and then it immediately divides into two main branches, the hyomandibular (B. II) and the superficial pterygoid (B. III), which supply the various muscles and tissues of the mental region and the postero-lateral part of the jaws.

According to RATHKE, the external carotid in Lacertilians arises very close to the "Kopfast," *i.e.*, the internal carotid, after the place where it receives the ductus caroticus, but in certain forms, including *Lacerta ocellata* and *L. agilis*, these two points are situated some distance apart. The condition in *Sphenodon* most nearly approaches that found in the *Lacertidæ*.

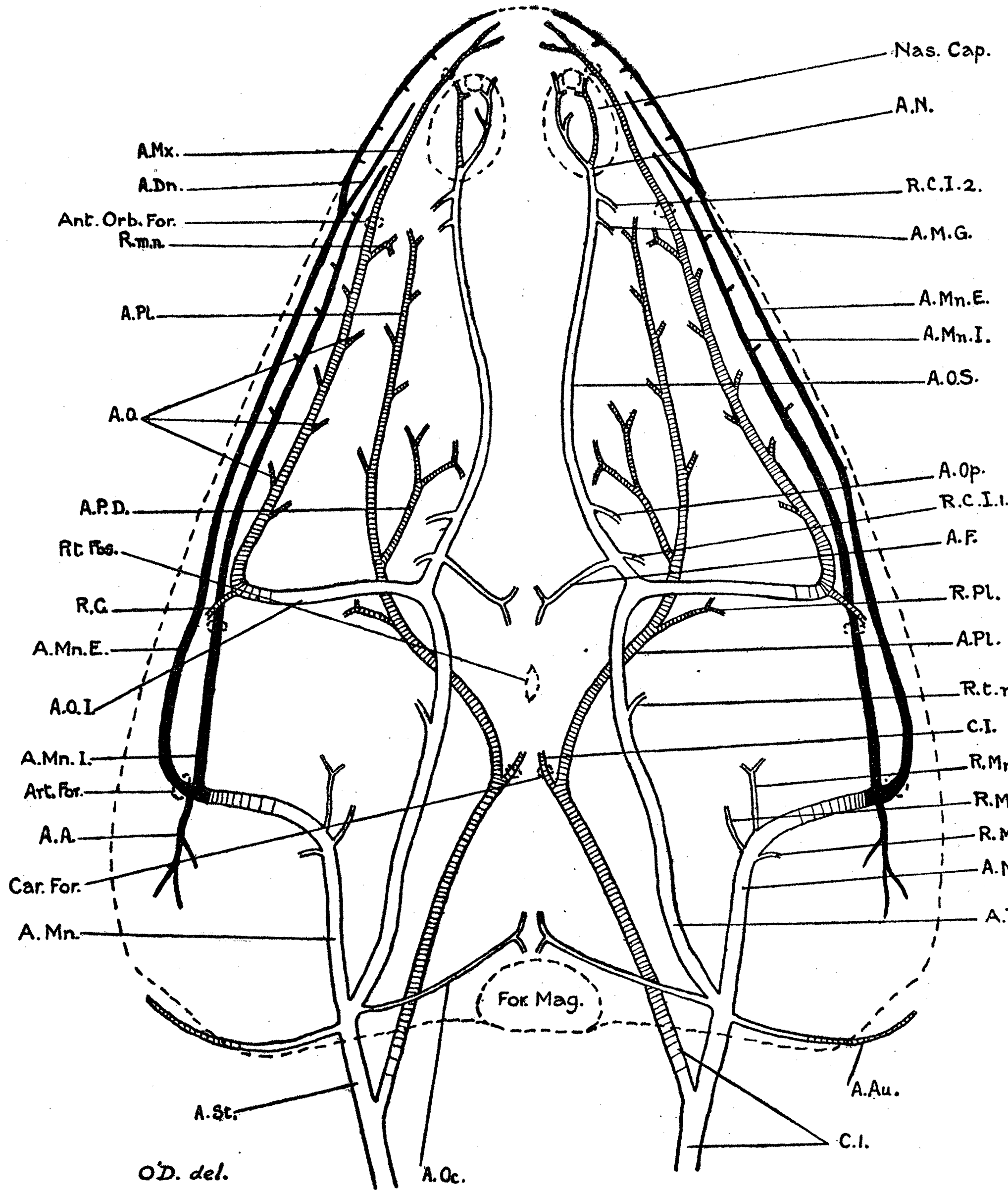
B. I. *Arteria thyreoidea superior* (V. BEMMELEN, 'Thymusdrusen Ast,' RATHKE).—The thyroid artery is a small vessel coming off from the external carotid immediately after the origin of the latter. It runs forwards and inwards, entering the lateral lobe of the thyroid gland.

RATHKE states that in the Lacertilia this branch may sometimes come from the external carotid and sometimes from the common carotid, but he erroneously calls it a thymus branch, as he had previously made the mistake of identifying the thyroid as a thymus gland. VAN BEMMELEN (10) gives two figures of this vessel in *Sphenodon*: in Plate I, fig. 1, it is depicted as arising from the common carotid, which, as far as my observations go, is incorrect; but in Plate I, fig. 6, he shows it correctly coming from the external carotid. The first of these figures, although very good in many ways, somewhat distorts the arteries in order to display the nerves, with which the author was more particularly concerned, and this may account for the inaccuracy.

B. II. *Arteria hyomandibularis* (A. sub-mentalis superficialis, CORTI (text-fig. 3)).—This is the inner and slightly larger of the two branches into which the external carotid divides. It gives off a glossopharyngeal branch (II. α) shortly after its origin, and then runs forwards along the inner border of the hyoideus muscle to its anterior end. Here it passes along the inner border of the end of the anterior cornu of the hyoid and then divides into two main trunks, a submandibular (II. β) and a genioglossal (II. γ).

B. II. α. *Arteria glossopharyngeus.*—The glossopharyngeal artery arises from the base of the hyomandibular and passes dorsal to the hypoglossal nerve to take up a position on its inner side. It accompanies this nerve forward, giving branches to the hyomaxillaris muscle, and on into the genioglossus muscle, to which it also gives branches. It can be followed along the outer ventral border of this muscle almost to its anterior end.

B. II. β. *Arteria sub-mandibularis* (text-fig. 7).—This is a well-marked vessel, situated on the outer ventral surface of the hyomandibularis muscle and running forward on its right to its anterior end at the symphysis menti.



TEXT-FIG. 3.—Diagram of the Main Arteries of the Head, exclusive of the Lower Jaw, viewed from above. Ventral arteries solid, dorsal arteries clear, and intermediate arteries shaded.

A.A., arteria articularis; *A.Au.*, arteria auricularis; *A.Dn.*, arteria dentalis; *A.F.*, arteria frontalis; *A.M.G.*, arteria musculo-glandularis; *A.Mn.*, arteria mandibularis; *A.Mn.E.*, arteria mandibularis externa; *A.Mn.I.*, arteria mandibularis interna; *A.Mx.*, arteria maxillaris; *A.N.*, arteria nasalis; *Ant.Orb.For.*, anterior orbital foramen; *A.O.*, arteriæ orbitales; *A.Oc.*, arteria occipitalis; *A.O.I.*, arteria orbitalis inferior; *A.Op.*, arteria ophthalmica; *A.O.S.*, arteria orbitalis superior; *A.P.D.*, arteria palatina dorsalis; *A.Pl.*, arteria palatina; *Art.For.*, articular foramen; *A.St.*, arteria stapedialis; *A.T.*, arteria temporalis; *Car.For.*, carotid foramen; *C.T.*, carotis interna; *For.Mag.*, foramen magnum; *Nas.Cap.*, nasal capsule; *Pit.Fos.*, pituitary fossa; *R.C.*, ramus coronoideus; *R.C.I.* 1 and 2, rami musculares of the arteria orbitalis superior; *R.m.n.*, ramus membranæ nictitantis; *R.Mn.* 1, 2, and 3, rami musculares of the arteria mandibularis; *R.Pl.*, ramus muscularis of the arteria palatina; *R.t.m.*, ramus temporo-masseteris.

It gives off branches to the adjacent musculature throughout the whole of its course, the largest of which are the following :—

II. β. i. The *Ramus musculo-mandibularis* is a large artery, passing outwards and upwards towards the inner surface of the mandible and dividing into two main branches, which enter the platysma muscle.

β. i. a. A *Ramus ventralis*, that is distributed to the main mass of the posterior part of the platysma muscle.

β. i. b. A *Ramus dorsalis*, that sends twigs into the deeper layers of the platysma and then runs along the inner surface of the mandible.

II. β. ii. The *Ramus muscularis* 1, a small artery that turns inwards and branches in the substance of the hyomaxillary muscle.

II. β. iii and iv. *Rami musculares* 2 and 3 also pass inwards but are distributed to the superficial and deeper layers of the genio-hyoideus muscle.

II. β. v–viii. *Rami musculares* 4–7, are distributed to the anterior portions of the platysma muscle.

II. γ. *Arteria genioglossa.*—The genioglossal artery leaves the main trunk at the level of the larynx and passes inwards and forwards along the side of the genioglossus muscle, to which it gives branches, to end just behind the mandibular symphysis.

B. III. *Arteria pterygoideus superficialis* (Plate 7, fig. 3, text-fig. 7).—The superficial pterygoid artery leaves the external carotid just after this vessel is crossed by the hypoglossal nerve and passes outwards. It gives off small branches to the ventral surface of the internal pterygoid muscle, along which it runs forwards, and at the anterior end of that muscle gives off one or two small branches to its dorsal surface. It is continued forward, branching repeatedly in the strip of subcutaneous tissue that lies between the hyomandibular muscle and the inner aspect of the mandible, and finally ends somewhere in the region of the anterior end of the hyoid (Processus entoglossus of OSAWA (62)).

C. *Carotis interna* (last part of Carotis communis, CORTI ; 'Kopfast des Carotidenbogens,' RATHKE) (Plate 7, fig. 3, text-fig. 3).—The internal carotid artery is a large artery, at least twice the diameter of the external carotid and, from the point of origin of the external carotid, it passes outwards and very slightly forwards over the ventral œsophageal wall. A little way along it bears on its posterior wall a small nodule, the carotid gland, and just beyond this receives the ductus caroticus (C. I). At this point it turns sharply forward, passing along the side of the œosophagus and is now, of course, the continuation forward of the old dorsal aorta of the embryo. Between the carotid gland and the point of entry of the ductus caroticus, the nervus laryngeus superior, a branch of the Vagus, loops around the internal carotid and runs forward up the neck. According to VAN BEMMELEN (10) the carotid gland communicates with the second thymus gland by a very fine strand of tissue. Unfortunately owing to the condition of the specimens I examined I have not been able to verify this observation.

A fairly large lymphatic vessel appears to enter the internal carotid on its ventral side at the same level as the ductus caroticus. This lymphatic trunk runs along the outer side of the internal carotid and alongside the vagus, passing under the internal jugular vein, and it is dilated just where it enters the carotid. The internal carotid continues forwards immediately below the second thymus and then outside the first thymus, at the anterior end of which it passes below the trunk of the hypoglossal nerve just as this is bending round towards the mental region. The artery then goes on, passing in succession superficially to the cervical sympathic nerve, the glosso-pharyngeal just as this curves outwards on the œsophageal wall, the internal jugular vein, and the vagus nerve. During this part of its course it gives off small twigs to the adjacent neck muscles, *e.g.*, the cucullaris, parieto-mandibularis, longissimus, etc.

Immediately after passing the vagus it gives off a very large trunk, the stapedial (B. II), and itself turns downwards and slightly inwards to run forward first on the lateral wall of the quadrate, then below the auditory capsule and finally on the base of the skull. Beneath the basisphenoid bone it gives off a fair-sized branch, the palatine (B. III), and then enters the cranial wall through the carotid foramen in the basisphenoid. It mounts in the wall of the sella turcica laterad of the hypophysis, to which it gives a small twig, and then in the substance of the cranial wall, which is here membranous, to a point just below the exit of the oculo-motor nerve and then turns inwards, becoming completely intra-cranial, to the latero-ventral wall of the brain. Here on the ventral surface of the crus cerebri it divides into an anterior (B. IV) and a posterior (B. V) branch. The distribution of these branches has already been worked out very carefully and fully by DENDY on the same specimens employed here, and is described in his paper on "The Intracranial Vascular System of Sphenodon" (22) and so need not be repeated.

C. I. *Ductus caroticus.* (Absteigender Schenkel des Carotidenbogens, RATHKE; junction of the Carotid and Aortic Arches, VAN BEMMELEN) (Plate 7, fig. 3, text-figs. 6 and 7).—This is a well-marked vessel of about the same calibre as the internal carotid itself. It runs from the postero-dorsal wall of the carotid, where it turns forwards immediately beyond the carotid gland, to the outer wall of the systemic arch a short distance in front of the ductus Botalli, thus putting the aortic and carotid arches in free communication with one another. Slightly nearer the systemic arch it gives off a moderate-sized branch (I. α), the muscularis cervicis. Some confusion exists in the nomenclature of this vessel, as it has been termed the ductus Botalli by BEDDARD (3, 7 and 8) in certain lizards, whereas it is more properly called the ductus caroticus, as it was first named by BRANDT (17). This matter, together with the distribution of the two ductus in Reptilia, I have dealt with more fully previously (60), and it is only necessary to call attention to one or two points therein mentioned. It is not found in the *Varanidæ* nor as an open vessel in the *Gekonidæ*. Although present in many other Lacertilians, it is very often reduced in diameter or even a solid strand, a ligametum caroticum, but in none of these is it less specialised than in *Sphenodon*.

The presence of both ductus caroticus and ductus arteriosus (Botalli) is a point of considerable importance. As they are to be found in the embryos of the Amniota, in adult Urodele Amphibia according to BOAS* (12, 13 and 14) and FRITSCH (28), and in the very young frog at the time of metamorphosis, we may justifiably conclude that the presence of both vessels in the higher forms indicates the retention of a fairly primitive condition. Indeed we may say, as has been pointed out elsewhere (60), "In this particular, as far as is known, *Sphenodon* is more primitive than any other living reptile."

C. I. α. *Arteria muscularis cervicis* (VAN BEMMELEN).—The cervico-muscular artery is a vessel running dorsally to supply the muscles in the region of the nape of the neck and the shoulders. According to VAN BEMMELEN it also gives off branches to the thymus glands, but I have not been able to verify this.

C. II. *Arteria stapedialis* (Carotis externa, CORTI; A. facialis, RATHKE) (Plate 7, fig. 2, text-fig. 3).—As has been noted already, the stapedial artery leaves the carotid just after this passes the Vagus nerve. It is a large trunk, considerably larger indeed than the continuation of the internal carotid, and its ramifications cover the whole of the temporal, orbital and a large part of the maxillo-mandibular region. The stapedial runs forward on the median side of the quadrate bone, between it and the cranial wall and then immediately ventrad of the columella auris. Just beyond the columella it gives off a small auricular twig (II. α) and then divides into two large almost equi-sized trunks, the temporal (II. β) and the mandibular (II. γ). Before it divides, the stapedial artery, which was ventral to the vena capitis lateralis, passes laterally around this vein so that the bifurcation takes place dorso-lateral to it.

C. II. α. *Arteria auricularis* (CORTI).—The auricular artery is a small vessel

* In as far as this statement refers to *Triton* and *Salamandra*, I have been able to confirm it by dissection.

which follows the chorda tympani along the posterior wall of the tympanic cavity. It passes along the posterior border of the second epibranchial, giving off in the tympanic region a small posterior tympanic artery which perhaps anastomoses with the external carotid artery.

C. II. β. *Arteria temporalis* (A. facialis, RATHKE) (Plate 7, fig. 2, text-fig. 3).—The temporal artery is slightly the larger of the two branches into which the stapedial divides. After giving off a small occipital branch (β. i) it passes upwards and forwards along the upper border of the cranium between the fascia of the longissimus muscle, to curve forward over the external pterygoid muscle. It gives off a small branch to the temporo-masseter muscle (β. ii) and at the anterior border of the pterygoid it splits into two main trunks, the supra-orbital (β. iii) and the infra-orbital (β. iv) arteries.

II. β. i. *Arteria occipitalis.*—The occipital artery is a small vessel running upwards in the longissimus muscle, to which it gives branches, on the side of the parietal bone. It divides into anterior and posterior branches.

II. β. ii. *Ramus temporo-masseteris.*—This is a small twig, supplying the similarly named muscle.

II. β. iii. *Arteria orbitalis superior* (RATHKE; A. orbito nasalis, GAUPP) (Plate 7, fig. 2, text-fig. 3).—The supra-orbital artery is a large one, continuing more or less in the line of the temporal. At the posterior end of the orbit it gives off three branches: one (iii. a) to the region of the frontal bone, another (iii. b) to the retractor muscle of the eye, and the third (iii. c), which runs outwards to the back of the eyeball, and is distributed to its muscles. The main trunk then continues forward in the dorsal wall of the orbit, and then penetrates the cartilaginous inter-nasal septum. In this it runs below the ophthalmic nerve, and leaves the septum again to re-enter the orbit at its anterior end. Here two branches are given off, one (iii. d) to the glands and muscles, and another (iii. e) to the inferior oblique muscle, and the artery goes on as the nasal (iii. f) into the olfactory capsule.

II. β. iii. a. *Arteria frontalis.*—The frontal artery is a small branch arising just behind the orbit. It runs upwards to the frontal bone, where it divides into an anterior and a posterior branch, supplying the superficial tissue.

II. β. iii. b. *Ramus muscularis* 1.—A fairly small artery, arising near the frontal, runs to the proximal part of the retractor bulbi muscle of the eye.

II. β. iii. c. *Arteria ophthalmica* (Plate 8, fig. 10).—The ophthalmic is a somewhat larger artery, running downwards on to the back of the eyeball. It is distributed to the muscles of the eye as follows:—

c. 1. A branch to the posterior rectus.
c. 2. A branch to the anterior part of the retractor bulbi.
c. 3. A branch to the superior rectus.
c. 4. A branch to the back of the eye.
c. 5. A branch to the anterior rectus.
c. 6. A branch to the inferior rectus.

II. β. iii. d. *Arteria musculo-glandularis.*—This runs downwards, giving off a backwardly directed twig to the sclerotic coat of the eyeball. Continuing, it passes through the superior oblique muscle, supplying it with a twig, and on into the Harderian gland, in which it breaks up.

II. β. iii. e. *Ramus muscularis* 2 runs straight downward, and is distributed to the inferior oblique muscle.

II. β iii. f. *Arteria nasalis.*—The remaining part of the supra-orbital may be termed the nasal artery, since it enters the olfactory capsule and is distributed mainly to the olfactory organ, although its terminal branches end in the subcutaneous tissue of the snout. On entering the capsule it divides into two main twigs, the superior and inferior nasal arteries. These run in the floor and roof of the nasal cavity respectively, supplying the mucous membrane and the end of the snout, as indicated above.

II. β. iv. *Arteria orbitalis inferior* (A. dentalis superior, RATHKE) (Plate 7, fig. 2, text-fig. 3).—The infra-orbital artery leaves the temporal at the postero-dorsal corner of the orbit, turning sharply downwards in its hinder membranous wall. In then runs on in the floor of the orbit, accompanying the infra-orbital branch of the trigeminal nerve. In this part of its course it gives off the coronoid (β. iv. a) branch and others to the surrounding tissues (β. iv. b) and nictitating membrane (β. iv. c). At the front end of the orbit it enters the maxilla through the anterior orbital foramen, and so becomes the maxillary artery (β. iv. d).

II. β. iv. a. *Ramus coronoideus.*—This vessel is given off from the infra-orbital just as it turns to run forward in the floor of the orbit. It breaks up into small branches, distributed to the tissue in the coronoid region.

II. β. iv. b. *Arteriæ orbitales.*—While passing through the orbit, the infra-orbital artery gives off small vessels to the adjacent tissue.

II. β. iv. c. *Ramus membranæ nictitantis.*—At the anterior end of the orbit the infra-orbital artery sends a branch upwards, to supply the nictitating membrane.

II. β. iv. d. *Arteria maxillaris* (RATHKE) (text-fig. 3).—The maxillary artery is really the continuation of the infra-orbital, but deserving of a special name, since it enters the substance of the maxilla by the anterior orbital foramen. It runs forward in the jaw for some way, and finally leaves it, by a foramen at the anterior end of the maxilla, just beneath the external naris, to terminate in the subcutaneous tissues of the snout. While running in the maxilla it gives off four or five small branches, which pass outwards through tiny foramina to the subcutaneous tissues of the upper lip.

C. II. γ. *Arteria mandibularis* (RATHKE) (Plate 7, fig. 2, text-fig. 3).—The mandibular artery passes forwards from the stapedialis along the cranial wall until it reaches a point just below the roots of the trigeminal nerve, when it turns outwards and passes between the internal pterygoid and temporo-masseter muscles, accompanying the mandibular branch of the fifth nerve. Small branches are given off to the temporo-masseter muscle (γ. i and γ. iii) and the internal pterygoid muscle (γ. ii). At the level of the mandible the mandibular artery divides into an internal (γ. iv) and an external branch (γ. v).

II. γ. i. *Ramus muscularis* 1.—A small artery leaves the main trunk just before it reaches the level of the roots of the fifth nerve. It passes outwards, and is distributed to the temporo-masseter muscle in that region.

II. γ. ii. *Ramus muscularis* 2.—A small branch is given off immediately before the mandibular takes up its position alongside the corresponding branch of the fifth nerve. This supplies the internal pterygoid muscle.

II. γ. iii. *Ramus muscularis* 3.—Another branch, arising shortly after the former, runs forward to the anterior part of the temporo-masseter muscle.

II. γ. iv. *Arteria mandibularis interna*.—The inner fork of the mandibular artery passes forward along the inner aspect of the mandible to the coronoid region. Here it enters the bone through a foramen on the inner side of the coronoid bone and continues forward, first in the bone itself, but soon in the deep Meckelian groove. Several twigs leave it during its course, and pass outward to the subcutaneous tissue of the lower jaw.

II. γ. v. *Arteria mandibularis externa* (Plate 7, fig. 2, text-fig. 3).—After parting from the foregoing, this artery gives off a small articular branch (v. a), and then passes through the mandible, *vid* the articular foramen, to the outer aspect of the jaw, where it turns sharply forwards. In the dentary region it gives off a small dentary branch (v. b), and then goes on to supply the remaining part of the lower jaw up to the symphysis, and also sends twigs to the subcutaneous tissue of the lower lip.

II. γ. v. a. *Arteria articularis* is a small vessel running backwards to the tissues in the articular region.

II. γ. v. b. *Arteria dentalis* is a small branch from the external mandibular that enters the substance of the mandible in the dentary region. It runs forward below the teeth, to which it sends shoots, and it also gives off a few twigs, which pass through the bone to the outside.

C. III. *Arteria palatina* (text-fig. 3).—As has been indicated above, the palatine artery arises from the internal carotid beneath the basisphenoid bone just before the latter artery enters the carotid foramen. At first the palatine runs near the middle line, accompanying the third cranial nerve, and some distance along gives off a muscle branch (III. α), by which time it has turned slightly outwards. At the level of the sub-orbital foramen, a dorsal palatine branch (III. β) is given off. The main trunk runs forward beneath the palatine bone, giving off numerous branches to the sub-mucosa of the roof of the mouth, and finally breaks up in the sub-nasal region.

C. III. α. *Ramus muscularis.*—This branch of the palatine artery passes outwards and forwards, to be distributed to the posterior wall of the orbit, and supplying a well-marked twig to the retractor bulbi muscle.

C. III. β. *Arteria palatina dorsalis.*—This takes a course forward dorsal to the palatine bone, and breaks up into a number of vessels, supplying the tissue in the vicinity.

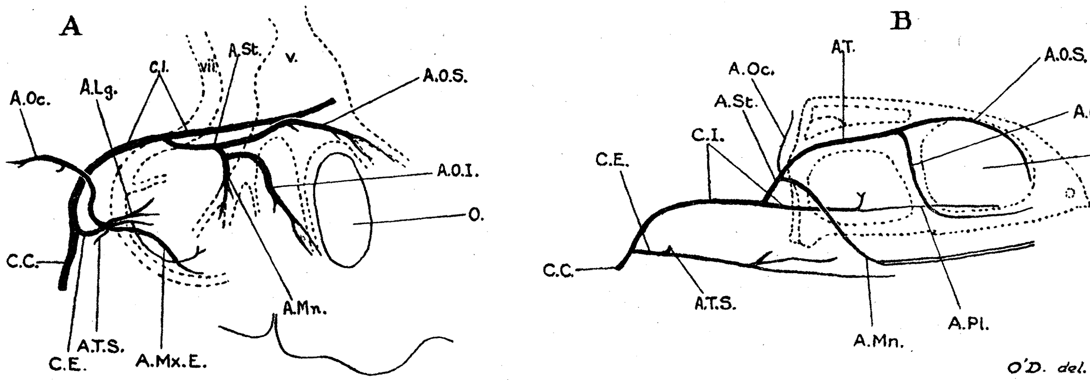
C. IV. *Ramus cranialis* of the internal carotid.

C. V. *Ramus caudalis* of the internal carotid.

These two branches forming the termination of the internal carotid artery and their intra-cranial distribution have already been fully described by DENDY (22), and are only mentioned here for the sake of completeness.

The Distribution of the Carotid Arteries (text-fig. 4).

It seems advisable at this point to call attention to the difference in the territories supplied by the internal and external carotid arteries in *Sphenodon* and the Mammalia respectively. In the mammal, the internal carotid is usually solely intra-cranial in its distribution, while all the remaining parts of the face and jaws are supplied by branches of the external carotid. The condition in *Sphenodon* is very different, however, for here the internal carotid serves not only the brain, but also the whole of the palate, face, and jaws, while the external carotid is relatively a much smaller and less important vessel, and is concerned mainly with the musculature of the lower jaw. At first sight this striking dissimilarity appears to indicate a fundamental difference between the two conditions, but the reason for it becomes clear in the light of TANDLER'S account (75) of the development of the carotid arteries in mammals. In the mammalian embryo we find the vessels arranged very much as in the reptile; indeed, it is interesting to notice that the arrangement in the 14 mm. human embryo according to EVANS (25) is essentially similar to that in *Sphenodon* and also to that in *Iguana tuberculata* according to RATHKE (67). The actual spatial relations are not the same, of course, owing to the very different proportions of the parts of the



TEXT-FIG. 4.—Diagrams for the comparison of the Internal and External Carotids of the Human Embryo and in *Sphenodon*.

A. Graphic reconstruction of the head arteries in a human embryo measuring 14 mm. Adapted from EVANS (25). B. Diagrammatic representation of the carotids in the adult *Sphenodon*. Approximate position of the skull indicated by dotted lines.

A.Lg., arteria lingualis; *A.Mn.*, arteria mandibularis; *A.Mx.E.*, arteria maxillaris externa; *A.O.C.*, arteria occipitalis; *A.O.I.*, arteria orbitalis inferior; *A.O.S.*, arteria orbitalis superior; *A.Pl.*, arteria palatina; *A.St.*, arteria stapedialis; *A.T.S.*, arteria thyreoidea superior; *C.C.*, carotis communis; *C.E.*, carotis externa; *C.I.*, carotis interna; *O.*, orbit; v and vii, primordia of the fifth and seventh cranial nerves.

head involved, the eye in *Sphenodon* being well in front of the brain, and the brain in the mammalian embryo being relatively larger. The most noticeable points of difference are that in *Sphenodon* the mandibularis artery arises nearer to the origin of the stapedialis (a change perhaps necessitated by the anterior position of the eye). The internal carotid gives off a palatine artery just before entering the skull, and the occipital artery is a branch of the temporal and not of the external carotid (this last difference, however, is not shown by *Varanus griseus*). Although the details of the branches of the external carotid then vary somewhat, the region supplied is essentially the same in each case.

In the mammalia in general an anastomosis is formed during the course of development between the stapedial artery and a branch of the external carotid, and with the later disappearance of the stapedial artery all its branches become transferred to the external carotid. Hence the difference between the regions supplied by the vessels in *Sphenodon* and mammals. The arteria stapedialis appears to persist in certain mammals, but even when it does, owing to the anastomosis, it gives up to the external carotid the mandibular artery as in the rat (TANDLER, 75), and in addition the infra-orbital artery in the case of the bat (GROSSER, 38).

The Systemic Arch (Plate 6, fig. 1, text-fig. 6).

As mentioned previously, HOCHSTETTER (44) dealt with *Sphenodon* in the course of a comparative account of the arteries of the alimentary canal. It is noteworthy that he considers the relation of these vessels in *Sphenodon* to be primitive and one from which other Lacertilian arrangements can be derived. BEDDARD (7) has furnished an account of the origin of the vessels coming from the systemic arch and the anterior part of the aorta. On the whole, the present work confirms that of these two writers, and also that of ZUCKERKANDL (82, 83, and 84) on the limb arteries. In spite of these works, no complete account of the systemic and aortic branches has yet been given.

The two systemic arches come off separately from the ventricle. The left systemic arch arises as the right ventral vessel of the three coming from the ventricle and it passes in a slight spiral twist over to the left, becoming more dorsal as it does so. The right systemico-carotid is slightly the largest and the most dorsal of the three trunks; it passes slightly to the left and becomes more ventral. As has been pointed out before, it gives off the carotids at the level of the anterior end of the atria, after which it becomes the systemic arch. From this point the courses of the two systemic arches are the same. Each vessel passes laterally and slightly forwards out on to the wall of the œsophagus; at the side of this it gives off a short branch, the anterior œsophageal (A), and exhibits a slight swelling of its wall, the œsophageal gland (VAN BEMMELEN, 10). Here the vessel turns downwards and inwards on to the dorsal wall of the œsophagus. It almost immediately receives on its anterior wall the ductus caroticus, and a short way beyond that the ductus arteriosus (ductus Botalli). The ductus arteriosus is a small vessel connecting the pulmonary and systemic arches. The systemic arches pass backwards and inwards and finally unite in the middle line to form the dorsal aorta. Dorsally to this junction the two sub-clavian arteries (B) are given off. Close examination shows, as BEDDARD (7) has pointed out, that the two arteries actually arise from the right systemic, but just at the point where it joins the left. In *Chamæleon*, according to MACKAY (54), the two sub-clavians arise well up on the right systemic arch. From its point of origin the dorsal aorta runs backwards in quite a normal way, giving off a number of branches (C–N). At the posterior end of the cœlom it passes on into the hæmal canal and as the caudal artery continues right down the tail.

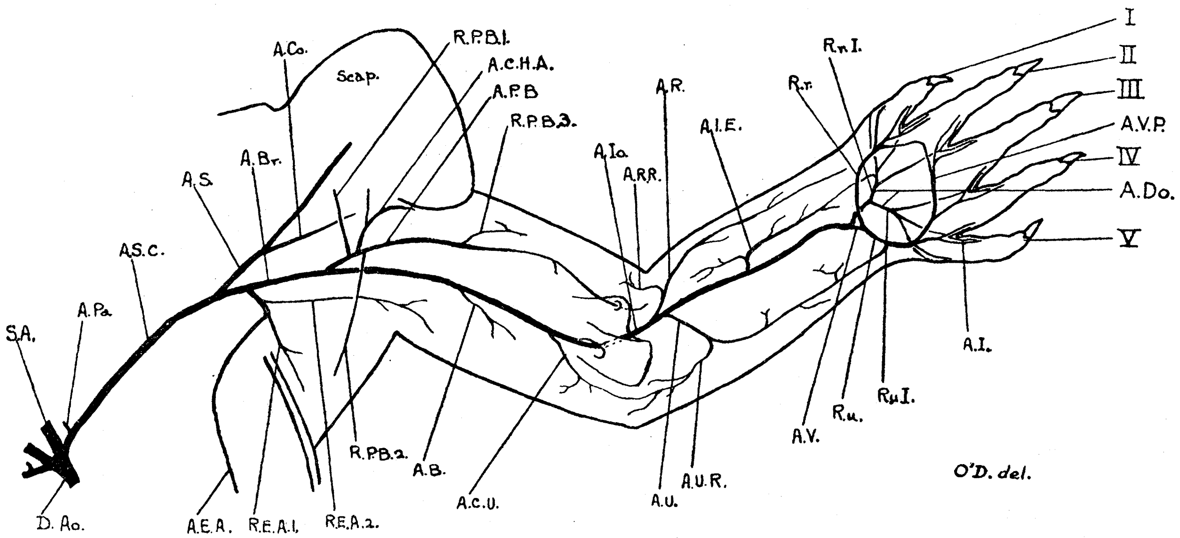
A. *Arteria œsophagea anterior.*—This is a small vessel running forwards up the side of the œsophagus from the systemic arch.

B. *Arteria subclavia* (CORTI) (text-fig. 6).—The origin of the sub-clavian artery has been described above. It passes outwards, giving off three branches

(B. I–III) and enters the arm, where it is termed the brachial artery. In its course along the arm to the entepicondylar foramen it gives off an arteria profunda brachii (B. IV) and other branches (B. V and VI). After passing through the foramen it issues into the muscles of the forearm, where it is termed the arteria interossea, and on its way to the carpus gives off branches (B. VII–X). It finally splits into two terminal branches (B. XI and XII) on the extensor surface of the metatarsals of the fore foot.

B. I. *Arteria parietalis.*—The first vessel is given off by the sub-clavian close to its origin, and is a parietal artery similar to those coming off from the aorta.

B. II. *Arteria scapularis* (CORTI).—This is a fairly large vessel going to the shoulder girdle. Its main stem forms a supra-scapular trunk, but it also



TEXT-FIG. 5.—Diagram of the Arteries of the Left Fore-limb from the Flexor Side.

A.B., arteria bicipitalis; *A.Br.*, arteria brachialis; *A.C.H.A.*, arteria circumflexa humeri anterior; *A.Co.*, arteria coracoidea; *A.C.U.*, arteria collateralis ulnaris; *A.Do.*, arcus dorsalis; *A.E.A.*, arteria epigastrica anterior; *A.I.*, arteriæ interdigitales; *A.I.E.*, arteria interossea externa; *A.Io.*, arteria interossea; *A.Pa.*, arteria parietalis; *A.P.B.*, arteria profunda brachii; *A.R.*, arteria radialis; *A.R.R.*, arteria radialis recurrens; *A.S.*, arteria scapularis; *A.S.C.*, arteria subclavia; *A.U.*, arteria ulnaris; *A.U.R.*, arteria ulnaris recurrens; *A.V.*, arteria volaris; *A.V.P.*, arcus volaris profunda; *D.Ao.*, dorsal aorta; *R.E.A.* 1 and 2, rami musculares of arteria epigastrica anterior; *R.P.B.* 1, 2 and 3, rami musculares of arteria profunda brachii; *R.r.*, ramus radialis of arteria volaris; *R.r.* 1, ramus radialis of arcus dorsalis; *R.u.*, ramus ulnaris of arteria volaris; *R.u.* 1, ramus ulnaris of arcus dorsalis; *S.A.*, systemic arch; *Scap.*, scapula; I, hallux; II—V, digits.

gives off twigs to the neighbouring muscles and also a coracoid artery (II. *a*).

B. II. *a*. *Arteria coracoidea.*—This is distributed to the musculature in the coracoid region.

B. III. *Arteria epigastrica anterior* (A. mammaria externa, CORTI) (text-figs. 5 and 6).—The anterior epigastric artery arises in the axillary region, and after giving off two twigs (B. III. α and β) passes ventrally along the second rib. It then turns caudally a little to one side of the mid-ventral line, and runs backwards towards the posterior epigastric and the two probably anastomose.

B. III. α. *Ramus muscularis* 1.—A small muscular branch of the epigastric runs to the proximal ends of some of the muscles on the posterior side of the brachium.

B. III. β. *Ramus muscularis* 2.—This is also a small vessel going to the inner sheet of the ventral region of the latissimus dorsi.

The main vessel now becomes the *Arteria brachialis* (text-figs. 5 and 6).

B. IV. *Arteria profunda brachii* (CORTI, ZUCKERKANDL (text-fig. 5)).—The distribution of this artery is fairly typical, the trunk and its branches supply the triceps, supra-coracoideus, coraco-brachialis, and the humeral insertion of the pectoralis, following the nomenclature of OSAWA (62). It gives off branches (B. IV. α, β, and γ) at the proximal end, and another as it passes down (B. IV. δ). Finally, it comes to lie beside the nervus radialis, and may be termed the collateralis radialis (ZUCKERKANDL). It passes with the radialis nerve through the ectepicondylar foramen.

B. IV. α. *Ramus muscularis* 1.—This is a small branch going to the coraco-brachialis muscle.

B. IV. β. *Arteria circumflexa humeri anterior* (CORTI ?).—This vessel passes around the head of the humerus and has approximately the same distribution as the anterior circumflex of CORTI, although it arises from the profunda brachii and not from the brachial artery.

B. IV. γ. *Ramus muscularis* 2.—A small branch runs backwards to the ventral part of the latissimus dorsi muscle.

B. IV. δ. *Ramus muscularis* 3.—A fairly small branch supplies the coraco-brachialis muscle.

B. V. *Arteria bicipitalis* (ZUCKERKANDL) (Plate 8, fig. 8, text-fig. 5).—A vessel arises about half way to the foramen and mainly serves the biceps.

B. VI. *Arteria collateralis ulnaris* (CORTI, ZUCKERKANDL) (text-fig. 5).—A smallish artery arises from the brachial just above the entepicondylar foramen, and runs close to the ulnaris branch of the nervus medianus. It apparently anastomoses with the recurrent ulnar artery.

The main vessel after passing through the foramen may now be termed the *Arteria interossea* (Plate 8, fig. 9, text-fig. 5).

B. VII. *Arteria radialis* (CORTI, ZUCKERKANDL) (text-fig. 5).—The radial artery arises from the main trunk, shortly after it has passed through the entepicondylar foramen and shortly below this point it gives off a branch (VII. α).

The greater part of its course lies in the sulcus radialis, but on nearing the carpus it becomes more superficial.

B. VII. α. *Arteria radialis recurrens* (CORTI, ZUCKERKANDL).—This runs backwards and supplies the muscles in the neighbourhood of the elbow.

B. VIII. *Arteria ulnaris* (CORTI, ZUCKERKANDL) (Plate 8, fig. 9, text-fig. 5).—The ulnar artery arises a little beyond and is more deeply situated than the radial, and after giving off a branch (VIII. α) runs near the ulnar nerve to the wrist, where it splits into two. The smaller dorsal vessel passes to the dorsal surface of the hand and the ventral forms a fairly typical *Arcus volaris profundis* in conjunction with a branch from the interosseus (*q.v.*).

B. VIII. α. *Arteria ulnaris recurrens.*—A twig passes backwards supplying the elbow muscles and anastomosing with the collateralis ulnaris artery (B. VI).

B. IX. *Arteria interossea externa* (ZUCKERKANDL) (Plate 8, fig. 8, text-fig. 5).—Rather nearer the wrist than the elbow the interosseus artery gives off a short branch, the external interosseus, which divides into proximal and distal branches that lie close to the dorsal branch of the nervus radialis. The descending branch anastomoses with the arcus dorsalis.

B. X. *Arteria volaris* (Plate 8, fig. 9, text-fig. 5).—When the interosseus artery reaches the ends of the radius and ulna it dives down on to the flexor surface of the hand and under the intermedium gives off a short volar artery. This, together with a terminal branch of the ulnar artery, gives rise to the deep volar arch which commences as two vessels, a radial (B. X. α) and an ulnar (B. X. β).

B. X. α. *Ramus radialis* (R. medianus, ZUCKERKANDL).—This passes outwards and sends a twig to the outside of the pollex, and one to split over the space between the first and second digits.

B. X. β. *Ramus ulnaris* (R. lateralis, ZUCKERKANDL).—The ulnar branch of the volar arch runs outwards, giving a twig to the outside of the fifth digit and three others. These split over the spaces between digits five and four, four and three, and three and two respectively. From the last of these branches an anastomosis runs to the last branch of the ramus radialis so forming a complete arterial ring in the palm.

The arteria interossea, after giving off the volaris as described above, returns through the carpus just in front of the os intermedium on to the extensor surface of the hand, and here breaks into the two branches (B. XI and XII) which constitute the *Arcus dorsalis.* This peculiar course of the interosseus from the extensor surface down between the ends of the radius and ulna on to the flexor side and then back again through the carpus is evidently primitive, since it is met with in the Amphibia.

B. XI. *Ramus radialis* (ZUCKERKANDL).—The radial branch of the arcus dorsalis receives the anastomosing twig of the external interosseus, and gives off branches to the outside of the pollex and other interdigital twigs to split over the spaces between digits one and two and digits three and four.

B. XII. *Ramus ulnaris* (ZUCKERKANDL).—The ulnar branch of the arcus dorsalis sends a twig to the outside of the fifth digit, and interdigital arteries to the space between five and four and between four and three.

C. *Arteriæ parietales* (text-fig. 6).—From the point of union of the two systemic arteries to form the dorsal aorta, paired parietal arteries come off from this common trunk. Excluding the pair given off from the sub-clavian arteries, seventeen or more usually eighteen pairs can be found before the point of origin of the iliac arteries.

D. *Arteria œsophagea* (HOCHSTETTER).—A small œsophageal artery arises just behind the third parietals.

E. *Arteria gastrica* (HOCHSTETTER) (text-fig. 6).—The gastric artery leaves the dorsal aorta about the level of the fifth pair of parietals and runs to the anterior end of the stomach.

F. *Arteria cœliaca* (HOCHSTETTER; Superior mesenteric, BEDDARD) (text-fig. 6).—The cœliac artery is a large vessel coming from the dorsal aorta near the tenth parietal artery. It is largely concerned with the supply of the stomach and liver, but also serves various other organs by means of a series of branches (F. I–VII), and continues as a large vessel supplying the posterior region of the stomach.

F. I. *Arteria lienalis minor.*—A small artery goes to the spleen.

F. II. *Arteria lienalis major.*—This is the main supply of the spleen.

F. III. *Arteria pancreatica major.*—This is the main vessel going to the pancreas, and shortly after its origin it gives off a small twig to the spleen.

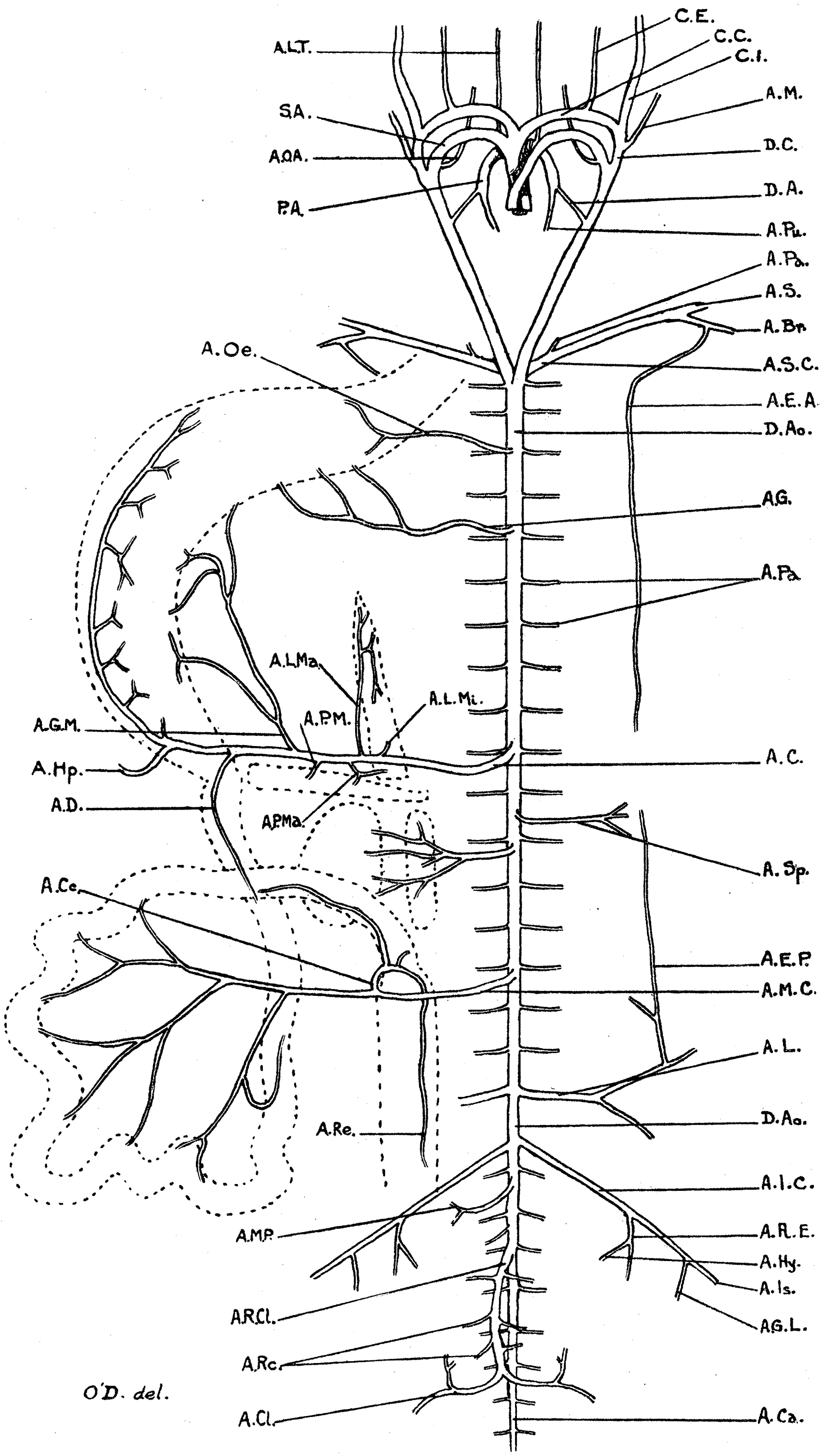
F. IV. *Arteria pancreatica minor.*—A second small twig also goes to the pancreas.

F. V. *Arteria gastrica medialis* (text-fig. 6).—This is a fairly large branch that almost immediately divides into two supplying the mid-region of the stomach. In some specimens the two branches appear to come off separately but close together from the main trunk.

F. VI. *Arteria duodenalis* (A. duodenalis superior, KLAATSCH).—The duodenal artery supplies the proximal part of the intestine.

F. VII. *Arteria hepatica.*—The hepatic artery leaves the main vessel just before it runs on to the stomach wall and enters the liver more or less ventrally.

G. *Arteria spermatica* (text-fig. 6).—This vessel runs to the supra-renal body to which it gives a number of branches, and another set of branches run on to the testis. The left arises a short distance in front of the right. Unfortunately



A.Br., arteria brachialis; *A.C.*, arteria cœliaca; *A.Ca.*, arteria caudalis; *A.Cc.*, arteria cœcalis; *A.Cl.*, arteria cloacalis; *A.D.*, arteria duodenalis; *A.E.A.*, arteria epigastrica arteria; *A.E.P.*, arteria epigastrica posterior; *A.G.*, arteria gastrica; *A.Gl.*, arteria glutea; *A.G.M.*, arteria gastrica media; *A.Hp.*, arteria hepatica; *A.Hy.*, arteria hypogastrica; *A.I.C.*, arteria iliaca communis; *A.Il.E.*, arteria iliaca externa; *A.Is.*, arteria ischiadica; *A.L.*, arteria lumbalis; *A.L.Ma.*, arteria lienalis major; *A.L.Mi.*, arteria lienalis minor; *A.L.T.*, arteria laryngeo-trachealis; *A.M.*, arteria muscularis cervicis; *A.M.C.*, arteria mesenterica communis; *A.M.P.*, arteria mesenterica posterior; *A.O.A.*, arteria œsophagea anterior; *A.Oe.*, arteria œsophagea; *A.Pa.*, arteria parietalis; *A.P.Ma.*, arteria pancreatica major; *A.P.Mi.*, arteria pancreatica minor; *A.Pu.*, pulmonary arch; *A.Rc.*, arteria recti; *A.R.Cl.*, arteria reno-cloacalis; *A.Re.*, arteria renales; *A.S.*, arteria scapularis; *A.S.C.*, arteria subclavia; *A.Sp.*, arteria spermatica; *C.C.*, carotis communis; *C.E.*, carotis externa; *C.I.*, carotis interna; *D.A.*, ductus arteriosus (Botalli); *D.Ao.*, dorsal aorta; *D.C.*, ductus caroticus; *P.A.*, pulmonary arch; *S.A.*, systemic arch.

Text-fig. 6.—Diagram of the Main Arteries of the Body Region in *Sphenodon*, with the alimentary canal pushed out to the right side of the animal. The dotted lines indicate approximately the position of certain of the viscera.

I have not had the opportunity of examining this vessel satisfactorily in the female, but doubtless as the ovary is disposed fairly similarly to the testis with regard to the supra-renal body the distribution of the vessel is much the same.

H. *Arteria mesenterica communis* (HOCHSTETTER) (Plate 6, fig. 1, text-fig. 6).—This vessel arises in the region of the fifteenth pair of segmental arteries, and I find that its distribution agrees more closely with the account given by HOCHSTETTER (44) than with that given by KLAATCH (50). The main trunk runs on to the upper part of the intestine and gives off a series of three or four large branches to the intestinal region. Soon after its origin it gives off a large factor (H. I) to the lower end of the intestine.

H. I. *Arteria cœcalis* (HOCHSTETTER).—After giving off a small twig to the junction of the intestine and rectum and a large one to the rectum (H. I. α) this artery runs along the end part of the intestine.

H. I. α. *Arteria recti.*—The rectal artery passes down along the dorsal wall of the rectum and anastomoses with the end of the posterior mesenteric artery.

J. *Arteriæ vasis efferentis.*—There are a series of three small vessels running to the vasa efferentia.

K. *Arteria lumbalis* (Plate 6, fig. 1, text-fig. 6).—The seventeenth or more usually the eighteenth parietal artery is much enlarged and constitutes a lumbar artery. It is distributed to the body wall and gives off two branches (K. I and K. II).

K. I. *Arteria epigastrica posterior.*—This posterior epigastric artery gives off a branch running inwards and forwards to the dorsal body wall and then itself continues on to the ventral body wall, where it turns and runs forwards and appears to anastomose with the anterior epigastric artery.

K. II. *Ramus muscularis.*—The muscular branch runs to the proximal ends of some of the muscles of the posterior surface of the thigh.

L. *Arteria iliaca communis* (GAUPP) (Plate 6, fig. 1, text-fig. 6).—This is a large artery supplying the hind limbs and it arises shortly behind the lumbar artery. It gives off an internal iliac artery (L. I) and then may be termed the external iliac artery. On reaching the limb it gives off a branch to the muscles of the proximal end of the thigh and the pelvic girdle (L. II). It then enters the leg and follows the ischiadic nerve and so may be termed the Arteria ischiadica (*i.e.*, the sciatic artery of many English text-books). Between the head of the femur and the knee it gives off several branches (L. III–VII). ZUCKERKANDL (84, p. 264) remarks that "Keine der hinteren Unterschenkelarterien kann ungeschwungen mit jenen der Säuger homologisiert werden," and the same is true also of the arteries of the thigh. Although he recognises internal and external circumflex arteries, for example, they both come off from the ischiadic and not from the femoral artery and they have not quite the same distribution.* The account of these branches down to the knee does not quite agree with that of ZUCKERKANDL, but the difference is slight and only in matters of detail. After passing the knee the main trunk, now termed by ZUCKERKANDL the Arteria interossea, gives off a deep branch to the flexor side (L. VIII), the lateral artery of that author. He also describes a further medial artery (VII. α) coming off at this point, but I have been unable to make it out satisfactorily. Almost immediately two arteries come off in succession; the first is a circumflex (IX) and the other a posterior muscular branch (X). The interosseus then runs on to the extensor side of the limb giving off an external interosseus (XI), after which it is bridged by a ligamentum tibio-fibulare, and on to the foot where it may be termed the Arteria dorsalis pedis. This gives off a vessel, the perforans plantaris (XII), which goes through on to the flexor side of the foot and then finally the main trunk breaks up into two terminal branches, an internal (XIII) and an external (XIV).

L. I. *Arteria iliaca interna* (GAUPP).—This artery supplies several of the muscles adjacent to its origin and gives off an important branch (L. I. α).

L. I. α. *Arteria hypogastrica.*—The hypogastric artery passes ventro-mesially to the wall of the bladder.

The main trunk may here be termed the *Arteria iliaca externa* (Plate 6, fig. 1, text-fig. 6).

L. II. *Arteria glutea* (GAUPP).—The gluteal artery supplies the muscles and tissues of the gluteal region and also a part of the proximal end of the hind limb.

The main trunk here becomes the *Arteria ischiadica* (Plate 8, fig. 4).

L. III. *Arteria circumflexa femoris externa* (ZUCKERKANDL) (Plate 7, fig. 4).—The external circumflex artery is a moderate sized vessel, running to the proximal external muscles of the thigh.

L. IV. *Arteria circumflexa femoris interna* (ZUCKERKANDL) (Plate 8, fig. 4).—The internal circumflex artery is a distinct branch, supplying the adductor and other internal muscles at the top end of the thigh.

L. V. *Ramus muscularis* 1.—This artery runs down on the inner side of the ischio-tibialis muscle, and in some respects recalls the profunda artery, but, unlike it, gives off a circumflex branch (L. V. α).

L. V. α. *Arteria circumflexa genu interna.*—A small artery passes round and supplies the muscles at the lower external end of the femur.

* The arteria ischiadica is normally replaced by the arteria femoralis as the main vessel of the leg of man, but it may persist and retain its original importance in certain instructive anomalous cases, as recorded by DUBREUIL (24), KRAUSE (51), and RUGE (71).

L. VI. *Ramus muscularis* 2.—Another artery arises from the ischiadic a short distance before the knee and passes to the deeper internal muscles.

L. VII. *Arteria circumflexa genu externa* (Plate 8, fig. 4).—This circumflex artery comes off immediately above the knee and passes round its external side.

The main trunk now becomes the *Arteria interossea* (Plate 8, fig. 4).

L. VIII. *Arteria tibialis lateralis* (Plate 7, figs. 4 and 5).—This is probably the artery described by ZUCKERKANDL (*loc. cit.*) as the lateral artery, for it accompanies the nervus tibialis posticus. It runs down to the plantar surface of the foot, and takes part in the formation of the arcus plantaris, together with a branch from the external tarsal, the tibialis medialis, the perforans plantaris, and the internal tarsal. The plantar arch gives off four branches, the arteriæ interdigitales, that split over the spaces between the digits. The first of the four anastomoses with the external tarsal, and a fifth branch runs to the outside of the hallux and anastomoses with a twig from the internal tarsal. The third and fourth of these arteries are also joined by an anastomosis across the base of the third digit. This showed clearly on one specimen, but not in others, and may be an individual variation. The perforans plantaris (XII) joins the plantar arch on the radial side at the point where the fifth branch, *i.e.*, that to the outside of the hallux, is given off.

L. VIII. α. *Arteria tibialis media* (Plate 8, fig. 5).—ZUCKERKANDL describes a medial branch coming off from the interossea at this point, and running down the tibia, with a large branch of the nervus tibialis, into the depths of the foot. I have not been able to find this vessel. There is, however, a small artery which appears to be a branch of the perforans plantaris, running up the distal end of the tibia with the nervus tibialis medius. This, as will be seen, corresponds with the end of the deep-lying medial artery of ZUCKERKANDL, and so may be the same vessel.

L. IX. *Arteria circumflexa genu interna inferior.*—The inferior circumflex artery of the knee comes off just below the articulation, and supplies the adjacent internal musculature.

L. X. *Ramus muscularis* 3.—A muscular branch runs externally, and probably supplies the peroneus and other adjacent muscles.

L. XI. *Arteria interossea externa* (Ramus dorsalis, ZUCKERKANDL) (Plate 8, fig. 4).—About half way to the ankle, near the interstitium interosseum, an external interosseus artery is given off, which is related to the main interosseus much in the same way as the corresponding vessel of the fore limb. It has two terminal branches, one of which runs up and one down the limb supplying the external muscles.

The main vessel now becomes the *Arteria dorsalis pedis* (Plate 8, fig. 5).

L. XII. *Arteria perforans plantaris* (Plate 8, fig. 5) (Ramus perforans plantaris, ZUCKERKANDL).—The perforans plantaris goes through the ankle between the distal extremities of the tibia and fibula on to the plantar side. Here, as pointed out above, it gives off the tibialis media (L. VIII. *α*, *q.v.*), and joins the arcus plantaris near the base of the hallux.

L. XIII. *Arteria metatarsalis interna* (Plate 8, fig. 4).—The internal tarsal artery soon divides into three branches. One anastomoses with the fifth branch of the plantar arch around the external side of the base of the hallux. The other two are *Arteriæ interdigitales*, splitting over the spaces between digits one and two and two and three respectively.

L. XIV. *Arteria metatarsalis externa* (Plate 8, fig. 4).—The external tarsal artery breaks into two *Arteriæ interdigitales*, which divide over the intervals between digits three and four and four and five. The latter of these gives off a branch, which anastomoses with the first branch of the plantar arch.

M. *Arteria mesenterica posterior* (HOCHSTETTER) (text-fig. 6).—This is a small but distinct artery coming off a little posterior to the ischiadic artery, and distributed to the dorsal wall of the rectum. It gives off a ramus ascendens, which probably anastomoses with the rectal artery (H. I. *α*, *vide supra*).

N. *Arteria reno-cloacalis* (text-fig. 6).—The reno-cloacal artery is a small, well-marked median vessel arising shortly behind the posterior mesenteric and passing between the kidneys, to which it gives branches (N. I). Near the posterior ends of these organs the vessel divides into two branches, the cloacals (N. II).

N. I. *Arteriæ renales.*—The renal arteries consist of about three pairs of vessels, running into the substance of the kidneys.

N. II. *Arteria cloacalis.*—The cloacal artery passes outwards, and is distributed to the lateral wall of the cloaca and extreme end of the rectum. It gives off a branch, which runs to the posterior margin of the cloaca.

After giving off the reno-cloacal artery, the dorsal aorta passes into the hæmal canal of the caudal vertebræ, and so becomes the *Arteria caudalis.* It gives off small paired parietal arteries to the muscles of the tail.

The Pulmonary Arch (text-figs. 1 and 6).

The pulmonary arch, the sixth of the embryonic series and the third of those remaining in the adult, is the most posterior and the most dorsal of the three. It arises well behind the anterior ends of the atria, and runs sharply dorsalwards and backwards, giving off a branch (A) to the larynx, trachea, and œsophagus, and (B) the pulmonary artery itself. From the point of origin of the pulmonary artery, only a short distance from the heart, the pulmonary arch continues outwards as a narrow, but nevertheless distinct, vessel, the ductus arteriosus or ductus Botalli, which runs into the systemic arch. This vestigeal vessel, whose significance has been pointed out previously (60), is present in an equally developed condition on both sides.

A. *Arteria laryngeo-trachealis* (Laryngeal artery, VAN BEMMELEN) (text-fig. 6).—This interesting vessel arises from the pulmonary arch a short distance from the heart. It was overlooked by RATHKE (66), who examined *Sphenodon*, but it was noted by VAN BEMMELEN (10), who also claims to have found it in *Platydactylus*, *Lacerta*, *Anguis*, *Pseudopus*, and *Iguana*. In company with the laryngeal nerves and the tracheal vein, it passes up the side of the trachea, to which it sends small twigs, finally breaking up in the larynx. It gives off a number of branches (I–VII).

The interest of this vessel lies in the fact that it is undoubtedly homologous with the arteria œsophagea of *Triton*, *Salamandra*, and *Spelerpes* as described by BETHGE (11). In these Urodela the respiration is carried on not only by the skin and lungs, but also by the mucosa of the buccal cavity and pharynx. Indeed, in *Speleropes*, where the lungs have been completely suppressed, it is performed entirely by the skin and the mucosa in these regions. We find as a result in this form that the pulmonary artery has disappeared, and the only branch of the pulmonary arch that remains is the very large œsophageal artery, which ramifies over the whole of the pharynx, œsophagus, and even the stomach. This relic of what is an important vessel in the Urodele Amphibia persists in certain Lacertilia as noted above, but appears to be best developed in *Sphenodon*.

A. I. *Arteria thyreoidea inferior* (VAN BEMMELEN).—This is a small artery going to the middle loop of the thyroid gland. VAN BEMMELEN (*loc. cit.*) remarks that he found this double arterial supply, partly from the pulmonary and partly from the carotid arches, going to the thyroid gland in all the Saurians he examined, but not in other Reptiles.

A. II–V. *Arteriæ œsophageæ* (Plate 7, fig. 3, text-fig. 7).—A series of small œsophageal branches are given off from the main vessel as it ascends the neck.

A. VI. *Arteria anastomotica* (text-fig. 7).—This is a small artery which anastomoses with its fellow ventrally to the posterior end of the larynx.

A. VII. *Arteria laryngea inferior* (text-fig. 7).—The inferior laryngeal artery breaks up into a number of twigs supplying the larynx and the genio-glossus muscle.

B. *Arteria pulmonalis.*—The pulmonary artery arises from the arch a short way beyond the laryngeo-tracheal artery and runs down the dorso-lateral border of the lung to which it is attached.

The Venous System.

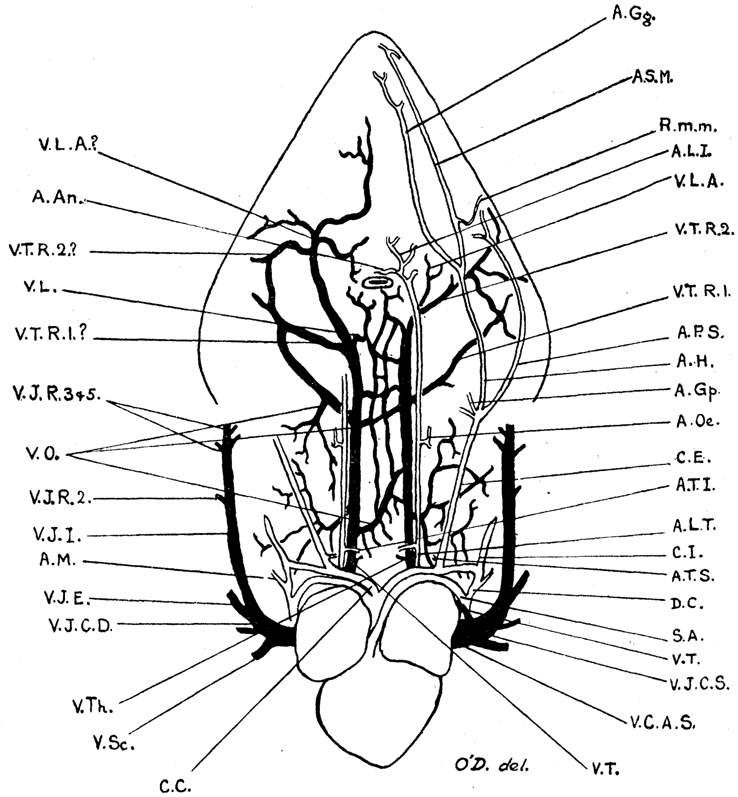
Considering the work that has been done on the vascular system of the Reptiles in general it is astonishing that there is nothing in the nature of a complete description of the venous system of *Sphenodon*, or of any Lacertilian. Even Corti, who has given such a detailed account of "*Psammosaurus griseus*," dismisses the veins in a couple of pages, remarking that he has neither successfully injected them nor dissected them out. Certain points have been dealt with in a fairly full manner, however.

Rathke (65) again provided the starting point of our modern knowledge by his account of the development of *Tropidonotus natrix*. This was added to by the work of Hofmann (47) on the development of the venous system in *Lacerta agilis*. Hochstetter (46) has dealt with the development of the veins in both *Lacerta* and *Tropidonotus*, but confined his attention mainly to the veins posterior to the heart, confirming and extending the observations of Hofmann. The development of the veins in the head and neck, again in *Lacerta* and *Tropidonotus*, have also been well described by Grosser and Brezina (40). Further, we have the interesting work on the cephalic vessels in *Lacerta agilis*, *Tropidonotus natrix*, and *Emys Europæa* by Bruner (18), in which he describes not only the vessels of the adult very fully, but also a muscular mechanism connected with them, whereby the venous blood pressure in the head can be raised. This is apparently called into action during the process of sloughing the skin. In addition to these more or less particular studies, a great number of comparative points have been cleared up in a valuable series of papers by Beddard (2–5, 7 and 8). Lastly, concerning *Sphenodon* itself, we have the work of Dendy (22) on the intra-cranial vessels, including the veins, so that as in the case of the arteries it is only necessary to indicate the relationship of the extra-cranial trunks to them. There is also a description of the sinus venosus in a paper by Röse (70).

As has already been indicated in dealing with the heart, the three main veins of the body, the two anterior and the single posterior venæ cavæ open into a distinct sinus venosus. The two procaval veins are similar in origin, and as the only differences between them are in the relative sizes of their constituent veins, it is only necessary to describe one of them in detail. In dealing with the venous system, the plan is often adopted of commencing with the smallest vessels and working gradually through the larger trunks to the heart. While this has certain advantages and indicates the direction of the blood flow, it is not the general method pursued in actual dissection. The vessels are usually found by following up the larger trunks away from the heart towards the periphery, and that is the plan adopted in the following description.

Vena cava anterior sinistra (Plate 7, fig. 3, text-fig. 7).—The left precaval vein is a short stout trunk opening into the dorsal side of the sinus venosus, and formed a short distance from the heart by the union of three veins, the tracheal (A), the common jugular (B), and the sub-clavian (C).

A. *Vena trachealis* (Grosser and Brezina, Bruner) (text-fig. 7).—The left tracheal vein runs from its point of entry into the left precaval vein, dorsal to the systemic and carotid arches, up the left side of the trachea. It receives tributaries (A. I–X) on its way to the larynx, some of which anastomose with their fellows of the other side and produce a venous network on the ventral side of the œsophagus. In the laryngeal region it receives further branches (XI–XII) from the muscles of the floor of the mouth. The constitution of the right tracheal vein is on the whole similar to that



Text-fig. 7.—Diagram to show the distribution of the Venæ Tracheales and adjacent Arteries. The trachea has been cut off close to the larynx and removed.

A.An., arteria anastomotica; *A.Gg.*, arteria genioglossa; *A.Gp.*, arteria glossopharyngeus; *A.H.*, arteria hyomandibularis; *A.L.I.*, arteria laryngea inferior; *A.L.T.*, arteria laryngeo-trachialis; *A.M.*, arteria muscularis cervicis; *A.Oe.*, arteria œsophagea; *A.P.S.*, arteria pterygoideus superficialis; *A.S.M.*, arteria sub-mandibularis; *A.T.I.*, arteria thyreoidea inferior; *A.T.S.*, arteria thyreoidea superior; *C.C.*, carotis communis; *C.E.*, carotis externa; *C.I.*, carotis interna; *D.C.*, ductus caroticus; *R.m.m.*, ramus musculo-mandibularis; *S.A.*, systemic arch; *V.C.A.S.*, vena cava anterior sinistra; *V.J.C.D.*, vena jugularis communis dextra; *V.J.C.S.*, vena jugularis communis sinistra; *V.J.E.*, vena jugularis externa; *V.J.I.*, vena jugularis interna; *V.J.R.I.*, rami musculares of v. jugularis interna; *V.L.*, vena laryngea; *V.L.A.*, vena laryngea anterior; *V.O.*, venæ œsophageæ; *V.Sc.*, vena subclavia; *V.T.*, vena trachealis; *V.Th.*, vena thyreoidea; *V.T.R.* 1 and 2, rami musculares of v. trachealis.

of the left, but the former is considerably larger and has more branches. In the embryo of *Lacerta*, according to both BRUNER (18) and GROSSER and BREZINA (40), a tracheal vein is present on both sides. During the course of development, however, anastomoses arise between them, no doubt corresponding to those in the adult *Sphenodon*, which allow of the complete disappearance of the posterior portion of the left vein in later stages. Thus it follows that in the adult only the right tracheal vein persists, as pointed out by PARKER (64), who, however, calls it quite wrongly (p. 161) the external jugular vein, and by VOGT and JUNG (78), who term it "die unpaare Kopfvene" (p. 714).

The condition in *Sphenodon* is noteworthy, since it is more primitive than that in *Lacerta*, and, moreover, represents a stage passed through by the latter animal in the course of its development. Further, the left vein in *Sphenodon* is much smaller than the right, as if foreshadowing its partial disappearance in other forms.

The vena trachealis in *Sphenodon* and *Lacerta* is an interesting vein, for, as will be seen from the above account, its distribution is very similar to that of the external jugular of the Amphibia, but at the same time it is obviously not the same vessel. In the frog, as is generally known, and in *Salamandra*, *Triton*, and *Spelerpes*, according to BETHGE (11), the external jugular is a fairly superficial vein running *ventrad* of the arterial arches and receiving two main tributaries, the vena lingualis and vena mandibularis. The tracheal vein in *Sphenodon* passes *dorsad* of the arterial arches and does not receive two such definite vessels, although it drains very nearly the same territory. There is present in the three Urodeles a vessel from which it seems easily possible to derive the vena trachealis of the Saurians, and that is the vena pharyngea (BETHGE). This vessel arises posterior to the arterial arches and its course lies dorsal to them along the wall of the pharynx. It will easily be seen then that anastomoses between it and the lingualis would enable it to take over the latter and through it the mandibularis, thus reducing the vena jugularis externa in *Sphenodon* (*q.v.*) to the unimportant vessel that it is.

A. I. *Vena thyreoidea* (text-fig. 7).—The thyroid gland is drained by a small vein entering the tracheal vein near its proximal end.

A. II–V. *Venæ œsophageæ* (text-fig. 7).—A number of veins come from the walls of the œsophagus. Some come inwards from the lateral wall and others outwards from the ventral wall. The latter take part in the formation of the venous network already described.

A. VI. *Ramus muscularis* 1.—This is a vein coming from the inner surface of the internal pterygoid muscle.

A. VII–X. *Venæ laryngeæ*.—The laryngeal veins are a series of small branches coming from the posterior muscles of the larynx. They anastomose with similar vessels from the right, and also have twigs from the anterior end of the œsophagus running into them.

A. XI. *Ramus muscularis* 2.—This is a fair-sized vein, running outwards from the side of the larynx and receiving three tributaries :—

XI. α. A branch that anastomoses with A. VI.

XI. β. A branch coming backwards from the lateral surface of the internal pterygoid muscle.

XI. γ. A branch coming forward from the same surface of the internal pterygoid muscle.

A. XII. *Vena laryngea anterior* (text-fig. 7).—The anterior laryngeal vein bends round the lateral wall of the larynx and receives three main branches :—

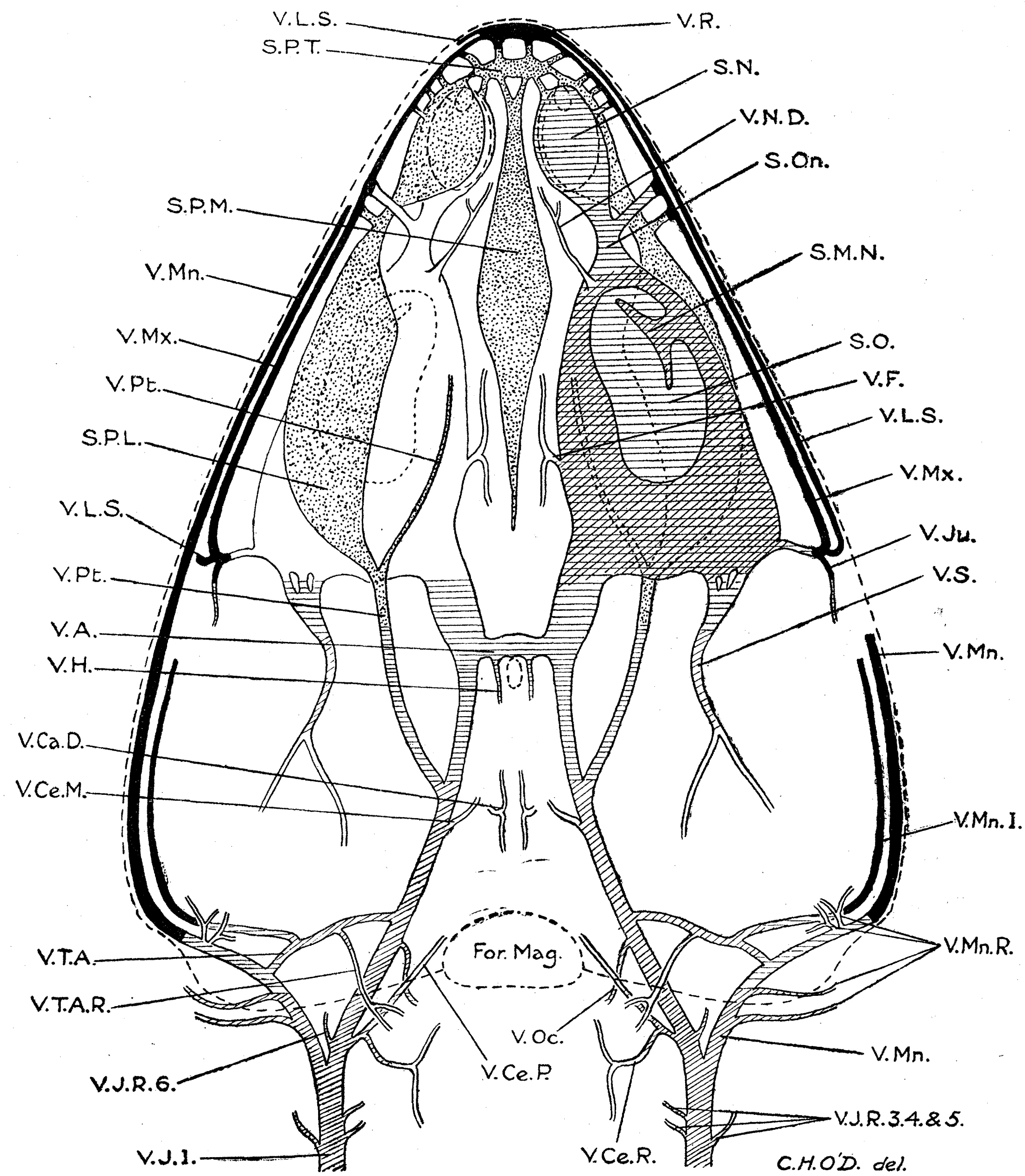
A. XII. α. A branch from the lateral and anterior walls of the larynx.

A. XII. β. A branch from the cerato-mandibular muscle.

A. XII. γ. A branch from the genio-glossus muscle.

B. *Vena jugularis communis sinistra* (V. jugularis, CORTI) (Plate 7, fig. 3, text-fig. 7).—The left common jugular vein is the second of the three trunks that unite to form the left precaval. From its origin it passes slightly laterally and then up the neck, receiving after a short distance a muscularis branch (B. I) and, a little more anteriorly, the external jugular (B. II). From this point it is continued forward as the *Vena jugularis interna* (V. jugularis, GROSSER and BREZINA ; V. jugularis interna, BRUNER), receiving a number of branches (B. III–VI) up to the hinder end of the neck, where it is crossed dorsally by the tenth cranial nerve and the internal carotid artery. Just at this point it receives the large mandibular vein (B. VII). A very short distance in front of this it receives a branch (B. VIII) on its outer side, and on the inner side, at the same level or just anterior to it, the posterior cerebral vein (B. IX). This is an important landmark, as the combined vessel formed by the main trunk up to this point and then continued on as the posterior cerebral vein is homologous with the internal jugular vein of the mammals, including man.

The constitution of the anterior end of the main trunk can only be properly understood in the light of its development. A marked difference between the venous supply in the head of the human embryo and of the adult was first pointed out by LUSCHKA (53), who, however, was not in possession of sufficient data to give a satisfactory explanation thereof. This line of enquiry was carried further by SALZER (72), who worked out the partial replacement of the old "anterior cardinal vein" (*sic*, really vena capitis medialis) in the head region by a more laterally situated trunk, which he termed the vena capitis lateralis. A further paper by



TEXT-FIG. 8.—Diagram of the Venous System of the Head. Vessels in jaws indicated in black. Palatine vessels dotted shading. Vessels at level of ventral side of cranium horizontal shading. Vessels at higher level oblique shading, and most dorsal vessels in outline only. On right side the mandibular vein is cut off short behind level of maxillary vein. The orbital and orbito-nasal veins are fully displayed. On left side the superior labial vein is cut off short at its origin, and the palatine sinuses fully shaded, while the orbital and orbito-nasal sinuses are indicated in outline or dotted outline only.

For.Mag., foramen magnum; *S.M.N.*, sinus membranæ nictitantis; *S.N.*, sinus nasalis; *S.O.*, sinus orbitalis; *S.On.*, sinus orbito-nasalis; *S.P.L.*, sinus palatinus lateralis; *S.P.M.*, sinus palatinus medius; *S.P.T.*, sinus palatinus transversus; *V.A.*, vena anastomotica; *V.Ca.D.*, vena capitis dorsalis; *V.Ce.M.*, vena cerebralis media; *V.Ce.P.*, vena cerebralis posterior; *V.Ce.R.*, ramus muscularis of vena cerebralis posterior; *V.F.*, vena frontalis; *V.H.*, vena hypophyseos lateralis; *V.J.I.*, vena jugularis interna; *V.J.R.* 3, 4 and 5, rami musculares of vena jugularis interna; *V.J.R.* 6, ramus muscularis of vena jugularis interna; *V.Ju.*, vena jugalis; *V.L.S.*, vena labialis superior; *V.Mn.*, vena mandibularis; *V.Mn.I.*, vena mandibularis interna; *V.Mn.R.*, rami musculares of vena mandibularis; *V.Mx.*, vena maxillaris; *V.N.D.*, vena nasalis dorsalis; *V.Oc.*, vena occipitalis; *V.Pt.*, vena pterygoidea; *V.R.*, vena rostralis; *V.S.*, vena supratemporalis; *V.T.A.*, vena tympanica anterior; *V.T.A.R.*, ramus muscularis of vena tympanica anterior.

GROSSER and BREZINA (40) gave an excellent description of the development of the vascular system of *Lacerta* and *Tropidonotus*, and lastly GROSSER (39) reviewed these changes in the vertebrate series. As far as these results apply to Reptilia and particularly Lacertilia, they may be briefly epitomised as follows :—In the fairly early embryo there are present two longitudinal veins in the head and neck. The first is the anterior cardinal vein, probably to be regarded as intimately related to the somites, and starting at their anterior end behind the auditory vesicle. It runs backwards into the Ductus Cuvieri. The second, the vena capitis medialis (GROSSER and BREZINA), lies on the base of the brain ventral to and slightly mesial to the primordia of the cranial nerves, and receives the orbital sinus. These two are connected by means of a more or less transverse vessel, the vena cerebralis posterior (GROSSER and BREZINA), shortly behind the primordium of the tenth cranial nerve. As development proceeds a series of vascular rings are laid down around the primordia of cranial nerves five to ten. The linking up of the outer portions of these rings constitutes another longitudinal venus trunk, the vena capitis lateralis (SALZER), which lies dorsal and slightly lateral to the nerve roots. The vena cerebralis posterior grows upwards and joins with its fellow to help to form the vena longitudinis cerebri, which also acquires two further connections, with the vena capitis medialis and later with the vena capitis lateralis. The hinder of these two connections, the vena cerebralis media (GROSSER and BREZINA), runs round behind the cerebellum and into the vena capitis medialis close by the ganglion of the trigeminus. The front vessel, the vena cerebralis anterior (GROSSER and BREZINA), begins at the epiphysis cerebri and passes behind the cerebral hemisphere into the vena capitis medialis just behind the orbit.

With the subsequent disappearance of the inner longitudinal vessel, the vena capitis medialis, and of the transverse portions of the venous rings, the definitive head vessel comes to consist of three parts. 1. The posterior part, derived from the old anterior cardinal vein, extends up to the vena cerebralis posterior. 2. The median portion from this point on to just in front of the ganglion of the trigeminus is derived from the vena capitis lateralis. 3. The remaining anterior part is the remnant of the vena capitis medialis and the orbital sinus.

The vessel so far described in the adult *Sphenodon* is the posterior part, *i.e.*, the persistent anterior cardinal. The *vena capitis lateralis* portion passes upwards and inwards to the posterior end of the skull, running under the paroccipital bone, dorsal to the columellar auris and dorso-mesial of the bifurcation of the stapedial artery, to form the temporal and mandibular arteries. Just behind the columella auris the occipital vein (B. X) enters the vena capitis lateralis, and in front of the columella it receives the anterior tympanic (B. VII. γ), which puts it in communication with the mandibular vein. It continues forwards under the paroccipital bone along the ventro-lateral wall of the auditory capsule, on which its position is faintly marked by a shallow inconspicuous groove, through the foramen between the quadrate wing of the pterygoid bone and the otic capsule (*i.e.*, the foramen for the hyomaxillary branch of the seventh cranial nerve, and termed by WATSON (79) in *Diademodon* the pterygo-paroccipital fossa). Passing dorsal to the roots of the facialis nerve it receives on its dorsal side the median cerebral vein (B. XI) just behind the splitting of the trigeminus, and this marks the end of the vena capitis lateralis portion.

The main trunk, now in its anterior or *vena capitis medialis* portion, runs on ventral of the roots of the trigeminus forwards near the mid-ventral line towards the orbital sinus. A short distance beyond the nerve the pterygoid vein (B. XII) enters the vena capitis medialis, and at the level of the front end of the hypophysis cerebri it receives an anastomosing vein (B. XIII) which puts it into communication with its fellow of the opposite side. Anterior to this the character of the vessel changes, and, from being a vessel with a definite wall, it becomes sinusoidal in nature. The actual vessel can be traced forwards for some distance on the dorso-mesial aspect of the musculus protrusor oculi, as figured by BRUNER (18) in *Lacerta*, but the orbital sinus extends postero-lateral of this and somewhat obscures the vessel. The sinuses ultimately merge into one large *Orbital sinus*, which, although a continuation of the main trunk, can be more conveniently dealt with separately. For the whole of this main venous trunk BRUNER (*loc. cit.*) employs the term vena jugularis interna, but, as pointed out above, only part of it is homologous with the similarly named trunk in the mammals, and, in front of that, we have to deal with at least two portions that are distinct developmentally.

B. I. *Ramus muscularis* 1.—This is a small vessel joining the common jugular close to the heart and coming from the adjacent dorso-lateral muscles. It is not present on the right side of one specimen with the venous system injected, and so may not be constant.

B. II. *Vena jugularis externa* (BRUNER) (Plate 6, fig. 1; Plate 7, fig. 3, text-fig. 7).—There is a well marked vessel joining the internal jugular low down in the neck to form the common jugular vein. This vessel, from its general disposition, is apparently the external jugular vein, but this cannot be regarded as definitely established without reference to its development, for, as has been pointed out previously, it has apparently yielded its lingual and mandibular branches to the tracheal vein (*q.v.*). I have not been able to ascertain whether it is connected with the external mandibular, as BRUNER (18) states the corresponding vessel is in *Lacerta*. This is not improbable, however, since it runs right up the neck ventro-laterad of the cervical nerves as far as the posterior region of the head, draining the superficial muscles and subcutaneous tissue.

The diminution in the functional importance of the external jugular vein in *Sphenedon* and *Lacerta* is interesting, since that vessel is of fair importance in the Amphibia, and is still more important in the Mammalia, where, if it is the same vessel, as seems probable, the external jugular drains the whole of the head and face, leaving practically only the brain to the internal jugular. In spite of the works of SALZER (72), and MALL (55), and SMITH (74), the question of the development of the external jugular vein in the Mammal does not appear to have been satisfactorily worked out. It is not merely that the external jugular in this order retains the factors that it has in the Amphibia, but it also adds to them in some way or other all the territory drained by the capitis lateralis and capitis medialis portions of the main head vein in such a form as *Sphenodon.*

As will be seen from the above accounts, the names Internal and External jugular vein have a very different significance in the different groups of Vertebrates, and the terms should not be employed unless carefully defined.

From this point the main trunk is the anterior cardinal portion of the vena jugularis interna.

B. III. *Ramus muscularis* 2 (Plate 7, fig. 3, text-fig. 7).—This is a vein coming from the cucullaris muscle. It receives a well marked factor, which comes in from the surrounding subcutaneous tissue and penetrates the muscle.

B. IV. *Ramus muscularis* 3.—This is a second twig, draining the anterior part of the cucullaris muscle.

B. V. *Ramus muscularis* 4.—A small vessel returns blood from the longissimus dorsi muscle, and probably also from the deeper layers of the cucullaris.

B. VI. *Ramus muscularis* 5 (Plate 7, fig. 3, text-fig. 7).—Another fairly small vessel comes from the antero-dorsal region of the cucullaris muscle.

B. VII. *Vena mandibularis* (V. maxillaris inferior, GROSSER and BREZINA; V. mandibularis, BRUNER) (text-fig. 8).—The mandibular vein is a well marked tributary, which joins the internal jugular at the point where the latter is crossed by the vagus. It is undoubtedly the same vessel as that described and figured by GROSSER and BREZINA (40), who, however, term it the inferior maxillary, a somewhat misleading name, since it has nothing to do with the maxilla. It passes outwards internal to the anterior cornu of the hyoid and posterior to the mandible, receiving two branches (B. VII. α and β). Just internal to the quadrato-jugal bone, an important tributary, the anterior tympanic vein (B. VII. γ) joins it, and, shortly after this, two twigs (B. VII. δ and ϵ) from the masetter muscle. The main trunk then takes its course along the outer surface of the mandible, finally entering the substance of the bone through a small foramen situated at the end of a short shallow groove. Just before so doing it receives a small external branch.

At this point it seems advisable to call attention to the interesting work of BRUNER (18), who has described a neuro-muscular apparatus connected with the bases of the vena mandibularis and the vena cerebralis posterior and the neighbouring part of the main trunk of the vena jugularis interna in various Lacertilia, Testudinata and Ophidia. It takes the form of a well-developed external muscular sheath, "the musculus constrictor venæ jugularis internæ," enervated by a special nerve supply, whereby the three vessels can be considerably constricted, and the venous pressure in the head greatly increased. The apparatus is useful, apparently, in helping in the operation of shedding the skin. The muscles are fairly easily seen in *Lacerta* and *Tropidonotus*, but are not quite so obvious in *Sphenodon;* they can be made very plain, however, in the following way. If the anterior region of the internal jugular, with a good piece of the ends of both mandibular and posterior cerebral veins, be dissected out, and any coagulated blood in them washed out and the preparation placed in a glass dish of alcohol containing a little glycerine, the muscles can readily be made out. When viewed by transmitted light, the ordinary parts of the vein wall appear moderately transparent and thin-walled, but, in the region occupied by the muscle, the walls of the vessels are very much thicker and more opaque. Transverse sections through the various regions also bring out quite clearly the fact that the bases of both mandibular and posterior cerebral vein, and of the internal jugular in the vicinity, are enveloped by a conspicuous coat of striate muscle, just as BRUNER described in other Saurians. The condition of the specimens did not allow of detailed examination of its nerve supply, but, as it lies quite close to the ganglion glossopharyngei, as in *Lacerta*, the nerves to the muscle, nervi tumefactores capitis, are doubtless fairly similar. For the same reason, the connection of the muscle with the skeleton, if present, could not be satisfactorily ascertained.

I also find myself in agreement with BRUNER with regard to the late appearance of these muscles during the course of development, for they are but feebly shown in the oldest stage I have examined (Stage S of DENDY).

B. VII. α and β. *Rami musculares* a and b.—These are two small muscular branches entering the mandibular vein in the region of the angle of the jaw from which they come.

B. VII. γ. *Vena tympanica anterior* (BRUNER) (Plate 7, fig. 2, text-fig. 8).—The anterior tympanic vein is an important tributary joining the mandibular a little further along its course. It passes mesially through the ear cavity anterior to the columella but behind the quadrate to enter the vena capitis lateralis just anterior to the point where it is crossed by the stapedial artery. Thus it forms an anastomosis between the mandibular and lateral head veins. In the region of the mandible it receives the internal mandibular (VII. γ. i), and dorso-mesiad of this a ventrally running branch (VII. γ. ii).

VII. γ. i. *Vena mandibularis interna* (BRUNER) (Plate 7, fig. 2, text-fig. 8).—The internal mandibular vein after leaving the anterior tympanic runs outwards below the quadrate bone and forward along the inner surface of the mandible, which it drains.

VII. γ. ii. *Ramus muscularis.*—This is a fair sized vessel bringing back blood from the anterior end of the longissimus muscle and the tissues in the region of the post temporal fossa.

B. VII. δ and ϵ. *Rami musculares* c and d.—These are two veins which almost immediately re-divide and drain the main mass of the temporo-masetter muscle.

B. VIII. *Ramus muscularis* 6.—This is a short branch from the parieto-mandibularis muscle.

B. IX. *Vena cerebralis posterior* (GROSSER and BREZINA ; V. cephalica posterior, VERSLUYS and DENDY) (Plate 2, fig. 2, text-fig. 8).—The posterior cerebral is a small but important vein which passes upwards and inwards from the internal jugular under the cucullaris muscle from which it receives a branch (B. IX. α). It takes up a position near the root of the tenth cranial nerve, and with it enters the skull through the jugular foramen. The distribution of this vein and its relations to other vessels within the cranium, where it receives a large posterior factor, the vena spinalis, has been dealt with fully by DENDY (22).

This last author proposes to call this vessel the *vena cephalica posterior*, following VERSLUYS (77), on the grounds that cerebralis is undesirable, as it has "nothing to do with the cerebrum proper" (*loc. cit.*, p. 413). I think on the whole it is better to retain the original terminology of GROSSER and BREZINA for several reasons. As a matter of fact, the adjective cerebral is usually employed in comparative anatomy to indicate a structure related to the brain as a whole, *e.g.*, cerebral carotid, while the term cephalic is used for a vessel related to the head. Thus, to extend the same nomenclature to the second of the transverse brain vessels, the *vena cerebralis media* of GROSSER and BREZINA, would lead to confusion, for median cephalic vein is a much closer translation of the *vena capitis medialis* of these authors, which is a totally distinct vessel. In the second place, VERSLUYS used the term *vena cephalica posterior* in error, probably misreading the lettering in the figures of the original authors, for he says (*loc. cit.*, p. 349): "Die andere kommt durch das Foramen magnum, dann zwischen Schädel und Atlasbogen hindurch aus der Schädelhöhle; GROSSER u. BREZINA haben sie 'Vena cephalica posterior' genannt." These investigators, however, nowhere use the term cephalica, but call the vessel in question the v. cerebralis posterior. Lastly, several subsequent writers, including GROSSER himself, in a comparative account of the head veins of Vertebrates (39), have employed the term cerebralis, which is now fairly widely accepted.

A rather striking difference is to be noted between the situation of the vena cerebralis posterior in *Sphenodon* and in *Lacerta* and *Tropidonotus*. In *Sphenodon*, as has been pointed out, the vein in question leaves the cranial cavity through the jugular foramen, and is in consequence homologous with the so-called internal jugular of mammals and birds. Both VERSLUYS (77) and GISI (34) state that they have been unable to find the posterior cerebral vein in *Sphenodon*, although the former points out that the canal leading from the foramen jugular is wider than would be necessary for the nerve alone. SCHAUINSLAND (73), however, has described the presence of a vein passing through the skull by the jugular foramen in company with the tenth and eleventh cranial nerves. As pointed out by DENDY (22), whose statement I am able to confirm, there is no doubt that the posterior cerebral vein leaves the skull through the foramen jugulare.

VERSLUYS (77), GROSSER and BREZINA (40), and BRUNER (18) are all in agreement that the posterior cerebral vein in *Lacerta* and *Tropidonotus* leaves the cranial cavity by the foramen magnum and not through the foramen jugulare. CLASON (20A) describes in *Lacerta* a fine vein passing through the jugular foramen, but this appears to be either an error in observation or the lizard in question was slightly abnormal, for, as will be seen later, this is also a possible explanation. HASSE (43) in *Tropidonotus* describes a vessel coming out through the foramen jugulare, but this has not been found by subsequent workers, *e.g.*, GROSSER and BREZINA (*loc. cit.*), BRUNER (*loc. cit.*), and O'DONOGHUE (58). It is stated that in all the Lacertilia dissected by VERSLUYS (*loc. cit.*), the vena cerebralis posterior came out by the foramen magnum with the single exception of *Amphisbæna fuliginosa*, in which there was also present a vein issuing from the jugular foramen. The two veins in this species enter the vena jugularis interna. This condition is an interesting one, for it is also realised in *Emys Europæa* (BRUNER), and as GROSSER and BREZINA point out is to be found in *Lacerta* embryo with a head length of 4·1 mm. A similar arrangement is probably to be found in the Crocodile, since RATHKE (68) mentions a vein leaving the cranial cavity in company with the tenth nerve, and another through the foramen magnum. His description is not at all easy to follow, however, and I agree with DENDY that the point must await further investigation. This loop on the posterior cerebral vein shows how it is possible for the two different conditions met with in *Sphenodon* and the Lacertilia to be arrived at, for it simply becomes a question of which part of the loop persists in the adult.

In Elasmobranchs the posterior cerebral vein leaves the skull with the tenth cranial nerve, as was pointed out in the embryo by GROSSER (39) and in the adult by O'DONOGHUE (59). The same happens in both Urodele and Anurous Amphibia according to REX (69), although there is some variation in the relative sizes of the venæ cerebrales posterior and media in this class. Furthermore, we find the vein leaving the skull with the tenth nerve in the Chelonia, according to HASSE (43), and as noted above also in Mammalia and Aves. There can be little doubt, then, that the condition in *Sphenodon* in this respect is more primitive than in the Lacertilia and Ophidia, and that it approximates more closely to the Urodele Amphibia.

Thus, although a vein of moderate calibre, the vena cerebralis posterior is of considerable morphological importance, since it is one of the most constant veins in the head of Vertebrata and serves as a valuable landmark.

B. IX. α. *Ramus muscularis.*—On its way beneath the cucullaris muscle, the posterior cerebral vein receives a branch from that muscle. It is formed by the union of an interior and posterior factors.

The main vessel now enters on its *Vena capitis lateralis* portion (Plate 7, fig. 2).

B. X. *Vena occipitalis* (Pate 7, fig. 2, text-fig. 8).—The occipital vein runs inwards and downwards from the lateral head vein, which it joins just behind the columella. It returns the blood from the muscles and tissues in the occipital region.

A short distance in front of this the main trunk receives the vena tympanica anterior, B. VII. γ, linking it up with the mandibular vein.

B. XI. *Vena cerebralis media* (Grosser and Brezina; Sinus transversus, Dendy) (Plate 7, fig. 2, text-fig. 8).—The intercranial course of this vessel has been dealt with by Dendy, who also describes its passage through the membranous cranial wall and downwards behind the epipterygoid bone into the end of the vena capitis lateralis just by the ganglionated root of the trigeminus. Intra-cranially it enlarges to form a big triangular sinus, and receives a branch, the vena capitis dorsalis (XI. α). Bruner (18) describes in the adult *Lacerta* a secondary extra-cranial connection between the median cerebral vein and the orbital sinus. I have not been able to discover any such vein in *Sphenodon.*

Although part of the median cerebral vein is extra-cranial in *Sphenodon*, it lies in close apposition to the membranous cranial wall down to the root of the trigeminus. There seems to be little doubt that it is completely homologous with the vein leaving the cranial cavity with the fifth nerve in such a form as *Ornithorhynchus*, in which the disappearance of the lateral membrane and the formation of a more external bony cranial wall has caused it to become completely intra-cranial. It appears to be a fairly widespread vein, as it occurs generally in the Amphibia, where it sometimes forms the main vessel leaving the cranium, and also in early Reptilia. In *Diademodon*, for example, it probably left the skull through the foramen described by Watson (79, p. 303) for the posterior two roots of the fifth nerve lying at the front end of the groove leading forward from the pterygo-paroccipital foramen.

B. XI. α. *Vena capitis dorsalis* (Bruner; Dendy) (text-fig. 8).—The dorsal head vein drains the muscles in the spino-occipital region, and just before piercing the skull to enter the median cerebral vein it receives an anterior factor from above the parietal bone, the *vena parietalis* of BRUNER. Apparently it passes through the skull by a small foramen in the parietal bone or between it and the pro-otic or supra-occipital regions. The exact position of this cannot be made out with certainty in an old skull. It enters the sinus transversus near its origin from the sinus (vena) longitudinalis. Mr. WATSON informs me that the entrance of a vena capitis dorsalis through a foramen or notch in the side of the hinder end of the brain case, either in the pro-otic or supra-occipital, appears to be a constant feature in early Amphibia and Reptilia, and the foramen is figured by him in Diademodon (79, p. 301). This is also noted by ANDREWS (1, p. 87) in Stenosaurus.

The main trunk now enters on its *Vena capitis medialis* portion.

B. XII. *Vena pterygoidea* (BRUNER) (Plate 7, fig. 2, text-fig. 8).—The pterygoid vein joins the lateral cephalic just in front of the trigeminus and the epipterygoid bone. It runs forwards and outwards in company with the palatine branch of the facial nerve and the palatine artery to the region of the sub-orbital foramen, through which it receives a large branch (XII. α). The main vessel continues on, passing towards the middle line again, and drains the dorsal surface of the palatine bone. The details of the finer connections at the anterior end cannot be made out satisfactorily by dissection, but are visible in a series of transverse and longitudinal sections of late embryos that Prof. DENDY kindly placed at my disposal.

B. XII. α. *Sinus palatinus lateralis* (BRUNER) (text-fig. 8).—The lateral palatine sinus enters the pterygoid vein near the sub-orbital foramen, through which it passes on to the ventral side of the palatine bone. At first a single trunk, it soon forms a sinusoidal network in the sub-mucosa of the palate, passing forward mesiad of the inner tooth row. Beneath the front end of the orbit it again runs together to form a single trunk, only to swell out shortly afterwards to form a large sinus beneath the nasal capsule. In this part of its course it anastomoses with the maxillary vein. Finally, right at the front end of the pre-maxillary region we find it takes its origin in a transverse sinus (XII. α (i)).

XII. α (i). *Sinus palatinus transversus* (BRUNER).—The transverse palatine sinus is a small vessel joining the two lateral palatine sinuses across the middle line, but it is important because of its connections. Laterally it runs into the maxillary vein, and through it is put into communication with a still more anterior transverse trunk, the rostral vein (B. XX). In the middle line the transverse palatine sinus receives the two openings of the median palatine sinus (α (i) a).

α (i) a. *Sinus palatinus medius* (BRUNER).—The median palatine sinus opens by two veins, which soon unite to form a single vessel. This passes back in the middle line and in the mid-orbital region forms a network of veins. Small vessels connect it with the lateral palatine sinus here and there.

B. XIII. *Vena anastomotica* (text-fig. 8).—This anastomosing vein joins the two median cephalic veins as they run along the membranous wall of the cranium just in front of the pre-sphenoid and in front of the hypophysis cerebri. It is a short vessel receiving on each side a branch—the lateral hypophyseal vein (B. XIII. α).

B. XIII. α. *Vena hypophyseos lateralis* (text-fig. 8).—This vein is here called lateral to distinguish it from the vena hypophyseos of BRUNER, which according to that author is connected with the median cerebral vein. It passes backwards inside the membranous wall of the hypophyseal cavity and apparently joins its fellow just behind the pituitary body. DENDY (22) was not able to find any vessel corresponding to the hypophyseal of BRUNER in the adult, nor does it appear to be present in the embryo.

Sinus orbitalis (BRUNER) (Plate 7, fig. 2, text-fig. 8).—Almost immediately in front of the anastomosis, the median cephalic vein becomes enlarged and sinus-like and so constitutes the orbital sinus. The foundation of our knowledge of this region in the Reptilia was laid by WEBER (80), although he took no notice of the veins leading into it. The exact limits of the sinus and point of entry of its tributaries are difficult to make out by dissection, but I have been much aided by the series of sections already mentioned. It is a very large vessel, extending from just in front of the anterior end of the hypophysis, where its hinder limits are marked by the fascia separating it from the temporal fossa, forward to the orbito-nasal septum. Through the fissura orbito-nasalis of GAUPP (32) it communicates with the nasal sinus (B. XIX. α). Its floor is formed by the smooth orbital muscle similar to that described by LEYDIG (52) in Lacertilia, and its internal boundary is the septum interorbitale. The sinus therefore occupies practically the whole of the orbit not taken up by the eyeball and its muscles, but it is incomplete dorsally save at the posterior end. Antero-mesially, although it passes up the septum, it only runs for a very short way along the roof of the orbit, and the same occurs antero-laterally, so that the sinus is much smaller at the front than at the back end of the orbit. Although it does not lie above the eyeball at the anterior end, it is in communication there with a subsidiary sinus in the nictitating membrane (B. XVIII). The main sinus by means of a series of tributaries (B. XV–XX) drains almost the whole of the anterior region of the head with the exception of the palate, and it also receives a posterior trunk from the supra-temporal region (B. XIV).

B. XIV. *Vena supra-temporalis* (BRUNER) (Plate 7, fig. 2, text-fig. 8).—The supra-temporal vein enters the postero-dorsal border of the orbital sinus slightly anterior to the anastomosing vein. It runs backwards first as a single stem, but afterwards divides into two in the tissue above the temporalis muscle quite close to the temporal artery and the nervus maxillaris nervus facialis of FISCHER (27). In the posterior part of its course it is sinusoidal in character, and the two vessels are probably connected by anastomosing trunks. It is probably the vessel termed supra-orbitalis by VOGT and JUNG (78), and its opening was noted by WEBER (80), who did not appreciate its significance, thinking it merely a short backward extension of the sinus.

B. XV. *Vena frontalis* (BRUNER) (text-fig. 8).—The frontal vein is formed by the union of anterior and posterior rami, which perforate the frontal bone and unite beneath it near the fronto-parietal suture to form a single vessel. This vein runs laterad of the taenia marginalis (GAUPP, 32) and enters the postero-mesial part of the orbital sinus. It drains the tissues overlying the frontal bone.

B. XVI. *Vena maxillaris* (BRUNER) (text-fig. 8).—The maxillary vein joins the orbital sinus at its postero-lateral corner. It passes outwards and then forwards in the body of the maxilla between it and the jugal; from the substance of the maxilla and its teeth it receives tributaries. Just before it enters the maxilla the labial vein (XVI. β) and the jugal vein (XVI. α) join it. In the region below the nasal capsule it comes out on to the external surface of the maxilla, and it receives in this part of its course two sets of anastomosing vessels, the one putting it into communication with the nasal sinus (B. XIX. α), and the other leading to the anterior network of the lateral palatine sinus (*vide supra*). Just beyond this it receives a small sinus, putting it into communication with the transverse palatine sinus (B. XII. α (i)), and finally it is joined again by the labial vein and immediately runs into the rostral vein (B. XX).

B. XVI. α. *Vena jugalis* (BRUNER) (text-fig. 8).—The jugal vein is a small twig coming from the tissues in the angle of the mouth.

B. XVI. β. *Vena labialis superior* (BRUNER) (text-fig. 8).—As pointed out above, the labial vein joins the maxillary just as it leaves the posterior end of the maxilla, and bending sharply round this bone runs forward in the upper lip. It drains the skin and subcutaneous tissue as it goes along, and rejoins the maxillary as the latter enters the rostral vein.

B. XVII. *Vena nasalis dorsalis* (BRUNER) (text-fig. 8).—The dorsal nasal vein is a small trunk that opens into the antero-mesial region of the orbital sinus. It draws blood from the skin and subcutaneous tissue above the nasal bones through which it passes.

B. XVIII. *Sinus membranæ nictitantis* (BRUNER) (Plate 7, fig. 2, text-fig. 8).—This sinus, which discharges into the anterior part of the orbital just laterad of the orbito-nasal sinus, lies partly in the nictitating membrane and partly in the Harderian gland, into whose substance it penetrates. It also probably receives twigs from the upper eyelid.

B. XIX. *Sinus orbito-nasalis* (Vena orbito-nasalis, GAUPP) (text-fig. 8).—The orbito-nasal sinus is a fairly large sinusoidal vessel, continuing on from the antero-mesial portion of the orbital sinus and draining the large nasal sinus (B. XIX. α), through a large foramen in the orbito-nasal septum. It anastomoses with the maxillary vein in the same region as the latter anastomoses with the lateral palatine sinus.

BRUNER does not describe a similar vessel in *Lacerta* nor in *Tropidonotus*, and, in my own observations (58), I was unable to find this vein in the snake. He states that the nasal sinus discharges by means of a sinus lateralis nasi into the maxillary vein. As just noted, this connection also exists in *Sphenodon*, not as a single vessel, but a series of veins. In *Sphenodon*, however, there is no doubt that the main drainage of the nasal sinus is *viâ* the orbito-nasal sinus. It is not easy to see why there is this difference between *Sphenodon* and *Lacerta*, unless it be that, in the latter form, where the orbit and nasal capsule are relatively further apart, this connection has been lost. It may probably be regarded as more primitive, since it occurs in the Amphibia as the orbito-nasal vein, GAUPP (31), and in *Scyllium*, O'DONOGHUE (59).

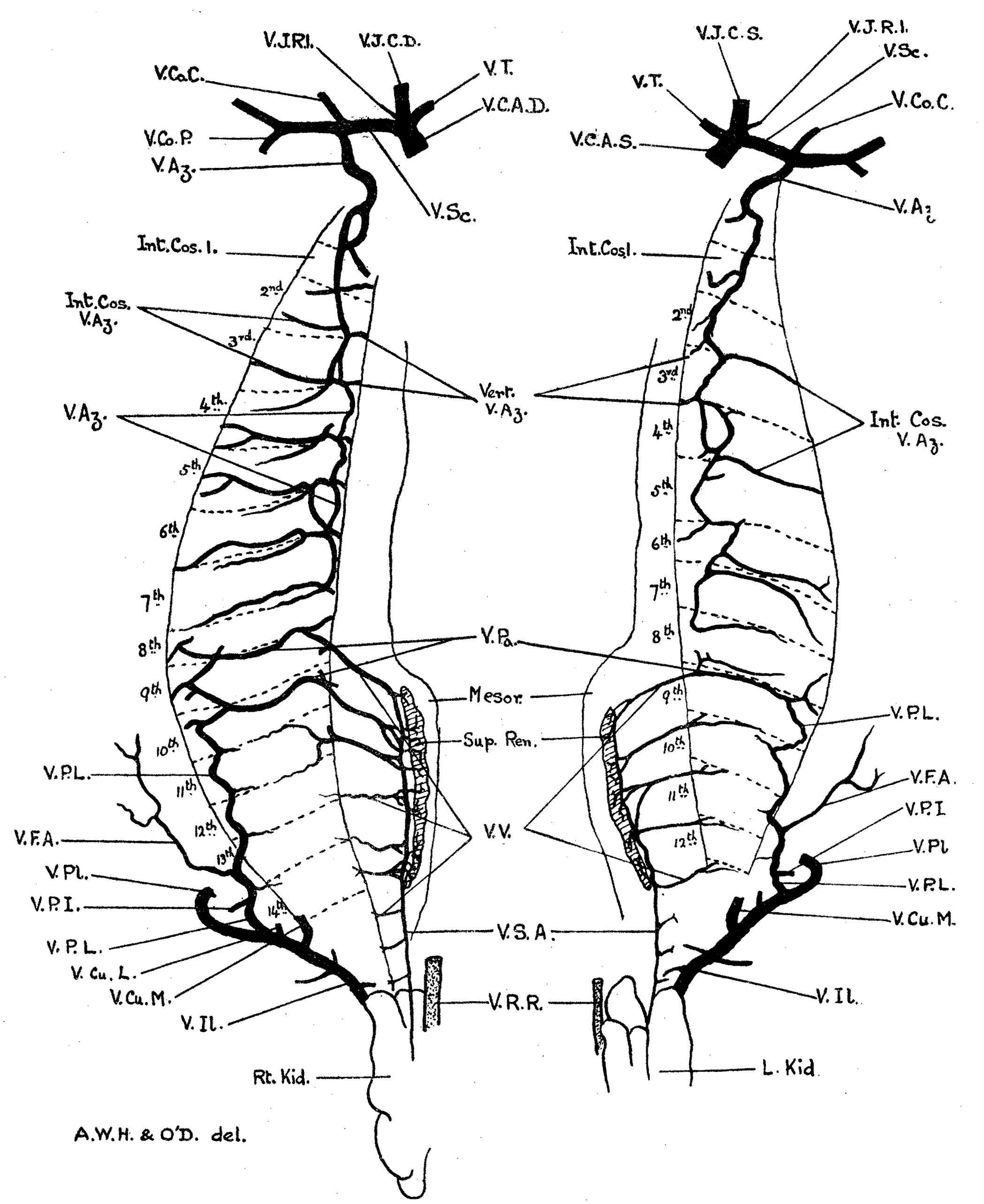
B. XIX. α. *Sinus nasalis* (Sinus vestibuli nasi, BRUNER) (text-fig. 8).—The nasal sinus of *Sphenodon* consists of a complex network of anastomosing veins of varying sizes. It ramifies intimately through the peculiar spongy tissue of this region described by LEYDIG (52) and BORN (15) in Lacertilia, who point out its likeness to erectile tissue. In this tissue, in *Sphenodon*, OSAWA (63) first noted the presence of smooth muscle fibres, a point later emphasised by BRUNER (18) in *Lacerta*, and one I am able to confirm. As previously stated, the nasal sinus communicates with the maxillary vein, and apparently with the transverse palatine sinus at its anterior end.

B. XX. *Vena rostralis* (BRUNER) (text-fig. 8).—The rostral vein is a small, irregular transverse vein surrounding the pre-nasal cartilage, and formed by a number of small twigs from the surrounding tissues. At its sides it opens into the maxillary veins in the manner already described, and so not only places them in communication with each other, but also is itself connected through them with the labial vein and transverse palatine sinus.

C. *Vena subclavia* (CORTI) (Plate 6, fig. 1; Plate 7, fig. 2, text-figs. 7 and 9).—The subclavian is the third of the great anterior veins that unite to form the pre-caval vein. It drains the fore limb, and, in addition, receives factors from the shoulder girdle and the ventral and dorsal body wall. Very little is known about the veins of the limbs in the Lacertilia, save a quite brief account of *Uromastix spinipes* given by HOCHSTETTER (46), with which the present account does not entirely agree, and I know of no reference to them in *Sphenodon.* They differ considerably from *Rana*, where, as has been fully described by GAUPP (31), two large venous trunks come from the upper arm, the brachial and the subclavian, so that it is hard to draw homologies between the two animals, and, as might be expected, *Sphenodon* differs considerably from the mammal. The subclavian is a large trunk that runs straight outwards from its point of union with the jugular and tracheal. A short distance along it receives on its anterior wall a factor (C. I) from the pectoral girdle, and the Azygos (C. II) enters it on the opposite side. About an equal distance further out it receives posteriorly another well-marked factor from the pectoral girdle (C. III), after which it may be termed the Vena axillaris. Just before entering the limb, the great cutaneous vein (C. IV) runs into it on the antero-dorsal side, and the main trunk, passing into the arm, becomes the vena brachialis. On its way to the elbow, along the superficial internal side of the upper arm, three large tributaries (C. V–VII) join it, and, after passing that joint, it becomes the vena antibrachialis superficialis of GAUPP. This passes slowly across the extensor side of the fore arm to its radial border, again receiving three well-marked branches (C. VIII–X), and, at the base of the hallux, turns mesiad, to form the arcus venosus dorsi manus. The arcus first gives off a vessel (C. XI) that anastomoses with its own distal extremity on the ulnar side, and then a series of venæ interdigitales (C. XII) to the spaces between the digits. Finally, it runs round on to the flexor side of the fore arm, and a short way up towards the elbow again, along the outer border of the "Anconæus quartus (richtiger quintus)" muscle of OSAWA.

C. I. *Vena coraco-clavicularis* (text-fig. 9).—The coraco-clavicular vein enters the anterior wall of the subclavian about 1 cm. before it flows into the anterior vena cava. It drains the dorsal part of the shoulder girdle, and passes ventrally between clavicle and coracoid and between the costo-scapularis and costo-coracoideus muscles. It receives a factor from the clavicular region.

C. II. *Vena azygos* (BEDDARD; V. vertebralis posterior, HOCHSTETTER) (text-fig. 9).—The azygos is a large interesting vein, entering the posterior wall of the sub-clavian nearly or quite opposite the coraco-clavicular. It can be traced backwards on both sides of the body to the posterior border of the seventh intercostal space. The factors joining it come from both the costal and vertebral regions, so that the territory it drains corresponds with that



TEXT-FIG. 9.—Dissection of Azygos, Iliac, Afferent Supra-Renal and Associated Veins on both sides.

Veins.—*Int.Cos.Az.*, intercostal branches of vena azygos; *V.Az.*, vena azygos; *V.C.A.D.*, vena cava anterior dextra; *V.C.A.S.*, vena cava anterior sinistra; *V.Co.C.*, vena coraco-clavicularis; *V.Co.P.*, vena coraco-pectoralis; *V.Cu.L.*, vena cutanea lateralis; *V.Cu.M.*, vena cutanea magna; *Vert.V.Az.*, vertebral tributaries of vena azygos; *V.F.A.*, vena flexoris abdominalis; *V.J.C.D.*, vena jugularis communis dextra; *V.J.C.S.*, vena jugularis communis sinistra; *V.J.R.I.*, ramus muscularis of vena jugularis communis; *V.Pa.*, venæ parietales; *V.P.I.*, vena pubo-ischio-trochanterica; *V.Pl.*, vena pelvica; *V.P.L.*, vena parietalis lateralis; *V.R.R.*, venæ renales revehentes; *V.S.A.*, vena supra-renalis advehens; *V.Sc.*, vena subclavia; *V.T.*, vena trachealis; *V.V.*, vena vertebralis.

*Int.Cos.*1., first intercostal space; 2nd–14th, second, &c., intercostal spaces; *L.Kid.*, left kidney; *Mesor.*, mesorchium; *Rt.Kid.*, right kidney; *Sup.Ren.*, dorsal surface of supra-renal body.

of the posterior cardinal of the embryo, and there is little doubt it is the actual remains of the anterior part of this. The posterior part of the embryonic post-cardinal probably persists as the afferent supra-renal, as will be discussed later. The break between the two is a very slight one in *Sphenodon*, for the factors of the latter vessel commence in the eighth intercostal space. There is, as far as can be seen, no actual connection between them such as HOCHSTETTER states he has found in Lacerta (46), and furthermore, I have not been able to find one or more venæ hepaticæ advehentes running from the azygos to the portal veins such as are described by the same author.

One of the earliest descriptions of this vessel in Lacertilia we owe to JOURDAIN (49), who describes it as "étendue depuis la jugulaire antérieure jusqu'à la queue," a description that is hardly accurate. According to PARKER (64), it is present only on the right side in *Lacerta viridis*, and this is perhaps substantiated by HOCHSTETTER (*loc. cit.*, p. 457), who terms it the vena vertebralis posterior, and says: "Das Blut aus der linkseitigen V. vertebralis posterior wird durch eine in dieser Gegend stärker entwickelte Queranastomose, von der bereits oben die Rede war, der V. vertebralis dextra zugeführt." The description of this author is not clear, however, for on the same page he apparently calls the vessel the A. vertebralis posterior and seems to suggest it is present on both sides.

Considerable variation in the presence and size of this vessel and the extent of its development on the two sides of the body is to be encountered in the Lacertilia, as has been shown mainly by BEDDARD. It may be present on both sides, and then, as a rule, one is considerably larger than the other. The better developed one may be on the left, as in *Varanus griseus* (8), *Iguana tuberculata* (2), and *Chamæleo sp.* (4), or on the right, as in *Pygopus lepidopus* (4). In yet other cases the vein is absent altogether on one side; the right in *Ophisaurus apus* (*Pseudopus pallasii*) (7); the left in *Phelsuma madagascariensis*, *Tarentola annularis* (4), and in *Heloderma suspectum* (8). The condition in *Sphenodon* is of interest because it is a primitive one, from which that found in any of the Lacertilia can be derived. In the first place, the two vessels are much more nearly of a size than in other forms, and, in the second, they extend back farther than most species, even where the two vessels are present in a fairly marked manner.

C. III. *Vena coraco-pectoralis* (V. thoracica anterior? HOCHSTETTER) (text-fig. 9). —This vessel comes from the ventral portion of the shoulder girdle and enters the sub-clavian vein laterad of the Azygos. The main trunk, which perhaps is homologous with the anterior thoracic of HOCHSTETTER, although it is not the only vessel coming from the girdle, may be regarded as the one passing out to drain the dorsal surface of the coracoideus and adjacent muscles. It receive two tributaries, one from the pectoralis muscle (C. III. α), and one from the sterno-coracoideus (C. III. β).

C. III. α. *Ramus pectoralis.*—The pectoral branch drains the dorsal surface of the pectoralis muscle and also picks up a well marked tributary from the ventral surface of the same.

C. III. β. *Ramus sterno-coracoideus.*—The sterno-coracoid branch comes from the internus superficialis and internus profundus portions of the similarly named muscle.

The main trunk may now be termed the *Vena axillaris*, as it accompanies the axillaris nerve.

C. IV. *Vena cutanea magna* (BETHGE) (Plate 8, fig. 8).—This vein enters the dorso-lateral extremity of the vena axillaris immediately before that vessel becomes the branchial vein. It comes in through the dorsal shoulder muscles from the external surface of the latissimus dorsi muscle, where it receives a small anterior tributary (C. IV. α). The main trunk passes backwards in the latero-dorsal subcutaneous tissue to the region of the pelvis, where it again dives through the musculature to enter the pelvic vein, thus forming a factor (A. III) of the system of the anterior abdominal vein (*q.v.*). This posterior connection is not quite the same as that described by BETHGE (11) in *Salamandra* and *Triton*, but the vessel appears from its general relation and distribution to be the same, so that I have adopted BETHGE's term of great cutaneous vein. It is not improbable that it will prove to be also homologous with the lateral cutaneous vein of the Elasmobranch (59).

C. IV. α. *Vena cutanea parva* (BETHGE).—The small cutaneous vein joins the great vein in the subcutaneous tissue dorsad of the latissimus dorsi muscle. It drains the tissue in the anterior continuation of the same line as the great vein and can be traced forwards to just behind the head.

The main trunk now enters the posterior aspect of the upper arm and so may be termed the *Vena brachialis* (Plate 8, figs. 7 and 8).

C. V. *Vena profunda brachii* (GAUPP) (Plate 8, figs. 7 and 9).—This is obviously not quite the same vessel as the profunda brachii of the frog, since in this animal the vein is a continuation of the subscapular, but as it has a very similar distribution it appears to be justifiable to give it the same name. It drains the cleido-humeralis, supra-coracoideus, anconæus and adjacent muscles, and receives near its end the Vena anastomotica longa (C. X).

C. VI. *Ramus muscularis* 1.—This branch runs into the radial side of the brachial vein just at the elbow, and comes mainly from the ends of the supinator and extensor digitorum communis longus muscles.

C. VII. *Ramus muscularis* 2.—This is the second muscular branch at the elbow, and it passes outwards superficially to the distal end of the anconæus and neighbouring muscles.

The main trunk now passes into the fore arm as the *Vena antibrachialis superficialis* of GAUPP, and is obviously the same vessel as that described by HOCHSTETTER (46) in *Uromastix* as "Eine veine im Sulcus radialis antibrachii" (Plate 8, figs. 7 and 9).

C. VIII. *Vena interossea* (GAUPP) (Plate 8, figs. 7 and 9).—The interosseal vein, probably the "Ulnare Randvene" of HOCHSTETTER, is a fair sized trunk coming off the superficial antibrachial, passing round on to the flexor surface of the proximal end of the radius and over towards the ulnar side of the limb. It runs down deep in the muscles, draining the flexor carpi ulnaris and pronator quadratus, into the hand. Unfortunately it could not be followed satisfactorily, but it appears to receive certain interdigital volar veins and to be connected with the main vessel on the extensor side by anastomoses, one of which is in the region of the bone of the hallux (*vide infra*).

C. IX. *Vena præhallucis* (GAUPP) (Plate 8, fig. 7).—This vein leaves the superficial antibrachial near the carpus and passes to the outside of the thumb, where it probably anastomoses with the veins on the palmar surface of the hand as just noted.

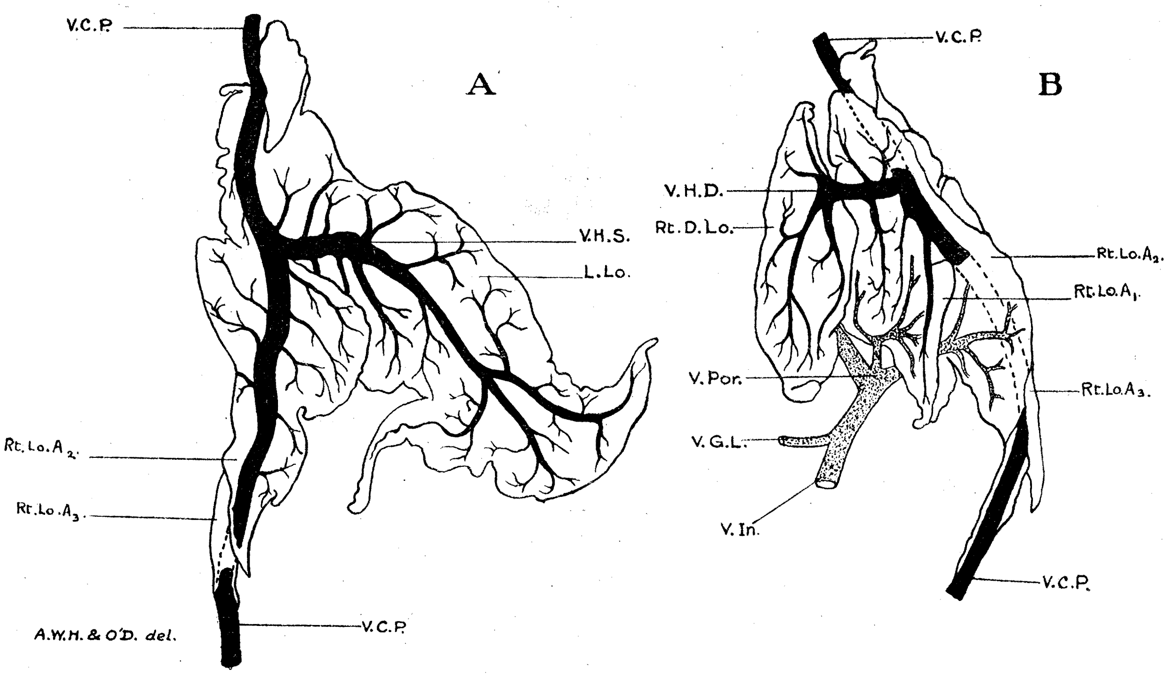
C. X. *Vena anastomotica longa* (Plate 8, fig. 7).—This long anastomosing vein comes off from the main vessel in the region of the distal end of the extensor carpi radialis longus muscle and runs right back up the fore arm and upper arm, following a course roughly parallel with that of the main trunk, but quite superficial. It flows into the brachial vein *viâ* the end of the vena profounda brachii (C.V) near the proximal end of the anconæus.

The main trunk now begins to turn across to the ulnar side of the hand, forming a well marked *arcus venosus dorsi manus.*

C. XI. *Vena anastomotica arcus venosi* (Plate 8, fig. 7).—This anastomosing branch comes off from the arcus venosus on the radial side and runs over the back of the hand, to enter the arcus again on its ulnar side.

C. XII. *Venæ interdigitales* (Plate 8, fig. 7).—Four well-marked interdigital veins are received by the arcus, each formed by the union of two lateral digital veins at the base of the space between each respective pair of digits. The fifth vein, corresponding to these, drains the external side of the fifth digit.

Vena cava posterior (Plate 6, fig. 1, text-figs. 10 and 11).—The post-caval vein is a large thin-walled trunk lying in the dorsal mesentery slightly to the right of the middle line and continuing in the line of the right efferent renal vein. It is formed by the union of two efferent renals (E) at the level of the posterior end of the left testis and passes forwards to the attenuated extremity of the right lobe of the liver. Partly embedded in this organ the vessel runs forward to its anterior end, receiving on its way a number of small hepatic veins and two much larger ones, a right (A) and a left (B). In front of the liver the post-caval vein passes freely forward in the mesentery to enter the posterior end of the sinus venosus. Posterior to the liver it receives the right spermatic vein (C), while the left spermatic vein (D) opens into the short anastomosis running transversely between the ends of the efferent renal veins.



TEXT-FIG. 10.—(*a*) Ventral aspect of Liver to show Post-Caval and Left Hepatic Veins. (*b*) Right side of Liver to show Post-Caval, Right Hepatic and Hepatic Portal Veins. The junction of the anterior gastric and anterior abdominal veins with the hepatic portal is hidden by the lobes of the liver.

Veins.—*V.C.P.*, vena cava posterior; *V.G.L.*, vena gastero-lienalis; *V.H.D.*, vena hepatica dextra; *V.H.S.*, vena hepatica sinistra; *V.In.*, vena intestinalis; *V.Por.*, vena portæ.

Rt.D.Lo., right dorsal lobule of liver; *Rt.Lo.*, A 1, A 2, and A 3, the three right ventral lobules of liver; *L.Lo.*, left lobe of liver.

A. *Vena hepatica dextra* (text-fig. 10).—The right hepatic vein is a fair-sized vessel composed of a number of factors from the various lobes of the liver on the right side. It enters the post caval about 3·5 cm. behind the point where this vessel leaves the anterior end of the liver.

B. *Vena hepatica sinistra* (text-fig. 10).—The left hepatic vein is smaller but very similar to the right, save that it comes from the left lobes of the liver and enters the left wall of the post caval just caudal to the point of entry of the right hepatic vein.

C. *Vena spermatica dextra* (Plate 6, fig. 1, text-fig. 11).—The right spermatic vein arises as a network of small vessels in the mesorchium at the anterior end of the testis. It then runs backwards along the supra-renal bodies, which it almost covers, receiving the efferent supra-renal veins (C. I), and also receiving as a rule four fair-sized veins from the testis. At the posterior end of the testis it turns sharply inwards and flows into the post-caval vein.

C. I. *Venæ supra-renales revehentes.*—These are a series of minute twigs coming from the supra-renal body, opening into the spermatic vein during its course along that gland and serving as efferent supra-renal veins.

D. *Vena spermatica sinistra* (Plate 6, fig. 1, text-fig. 11).—The relations of the left spermatic vein to the corresponding supra-renal body and testis are similar to those on the right, save that, as a rule, it has five branches from the testis instead of four. It does not open directly into the post-caval vein, but into the transverse anastomosis joining the left efferent renal to the right.

D. I. *Venæ supra-renales revehentes.*—A series of efferent supra-renal veins, similar to those on the right, open into the left spermatic vein.

E. *Venæ renales revehentes* (HOCHSTETTER) (Plate 6, fig. 1, text-fig. 11).—The efferent renal veins commence in the substance of the kidneys at their posterior ends and run forward as fair-sized thin-walled vessels on the median borders of their ventral faces and separated from one another in the middle line by the dorsal mesentery. The right vein, from the start, is much larger than the left, a condition that is common in the Lacertilia (*vide* BEDDARD, 7), and the two are joined by four large inter-renal anastomoses. Herein *Sphenodon* differs from both *Lacerta viridis*, *L. ocellata*, and *Varanus arenarius*, in which, according to HOCHSTETTER (46), there is only one small anastomosis at the posterior end of the kidneys. Between the kidneys and the place where they join one another, both veins receive a number of small tributaries from the mesentery. As already stated, the left efferent renal pours its blood into the right at the level of the hinder end of the left testis, by means of a short stout anastomosis into which the left spermatic vein runs.

The remaining veins of the body are not concerned with taking the blood back directly to the heart, and so can be dealt with conveniently as a series of distinct but often closely related systems.

The Supra-renal Portal System.

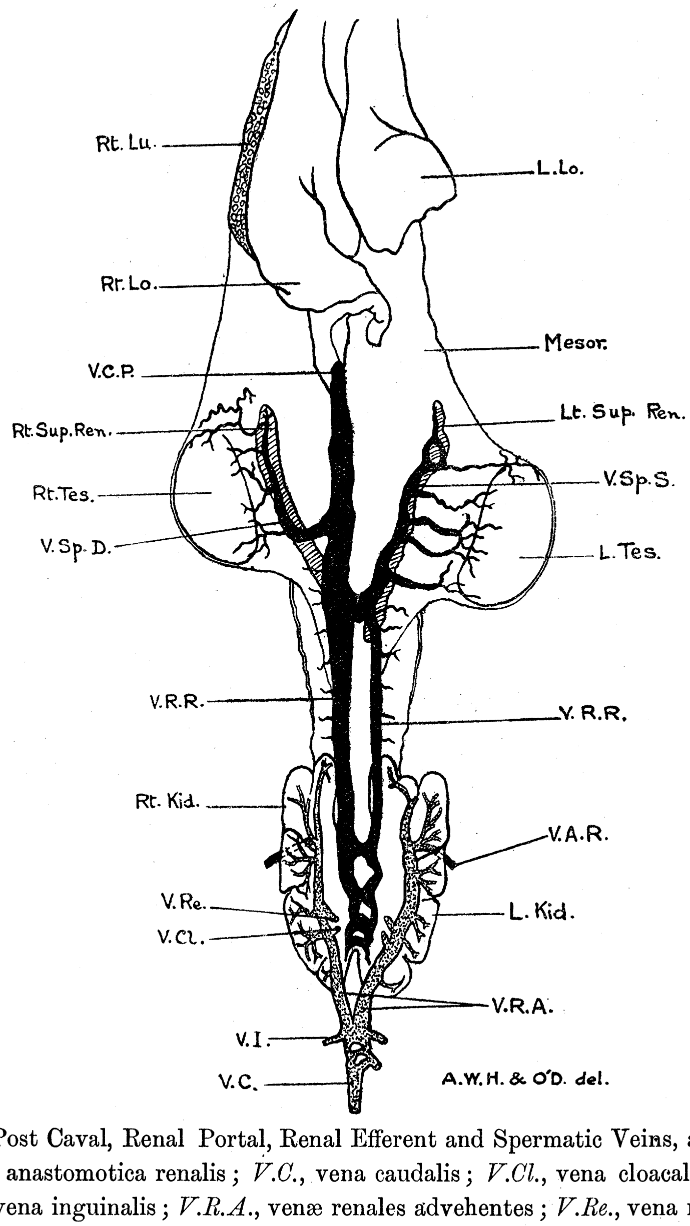
The presence of this system has already been noted in the *Varanidæ* by CORTI (21), HOCHSTETTER (46), and BEDDARD (8), in which genus it is very well developed. It is subject to a great deal of variation in the Lacertilia, as BEDDARD has shown, and, although usually present and often well marked, as in the *Varanidæ*, *Iguana* *tuberculata* (2), *Ophisaurus apus* and *Amphisbæna brasiliana* (7),* it may be considerably reduced, *e.g.*, *Tiliqua scincoides* (2), or even absent altogether, save as an abnormal variation, as in *Chamæleon vulgaris* (4). In *Sphenodon* it has apparently retained more primitive relations than in the other forms described, and this throws useful light on the question of its constitution. Its main factor is a vessel, termed by HOCHSTETTER (46) the Vena deferentialis, since it accompanies the vas deferens, and by BEDDARD (7) the post cardinal vein. With regard to this vessel, BEDDARD, after pointing out that it receives branches from the parietes, adds: "Considering . . . . the relation of the vein to the vas deferens (Wolffian duct), I imagine that it is to be regarded as a persistent, though small, posterior cardinal vein." The position of the vessel in *Sphenodon*, I think, fully supports this interpretation. The azygos vein, Vena vertebralis of HOCHSTETTER, is generally admitted to be a persistent part of the embryonic posterior cardinal vein, and it receives factors not only from the parietes, but also from the vertebral region. It will be seen that the vein in question similarly has parietal and vertebral branches at its anterior end, and, indeed, the break between it and the azygos on both sides is very small, being only from one vertebra to the next. In *Lacerta viridis*, as figured by HOCHSTETTER, it would appear as if there is not even this hiatus. Moreover, the posterior end of the vein disappears in the kidney substance as the old posterior cardinal would. Then again, in *Varanus arenarius*, HOCHSTETTER (*loc. cit.*, Plate 16, fig. 16) depicts the vein as opening into the anterior end of the afferent renal, and so directly continuous with the caudal vein. There seems to be little doubt, then, that this vessel is actually a persistent, though much reduced, portion of the posterior cardinal vein.

A. *Vena supra-renalis advehens* (V. cardinalis posterior, BEDDARD; V. deferentialis, HOCHSTETTER) (text-fig. 9).—The term afferent supra-renal vein seems preferable to posterior cardinal, as employed by BEDDARD, since the vessel is only a small part of the embryonic posterior cardinal, while the azygos is a larger persistent portion of the same trunk, and so more deserving of the name. The term vena deferentialis of HOCHSTETTER is open to the objection that it is obviously unsuitable in the case of the female. Afferent supra-renal is free from both these objections, and at the same time indicates its anatomical relation to the supra-renal gland by pairing it with the efferent supra-renal veins. In *Sphenodon* the vessel arises in the anterior end of the kidney, and passes forwards alongside the vas deferens to the anterior end of the supra-renal body to the substance, of which it gives off a large number of small twigs. Along its course it receives factors from the vertebral region (A. I), and also from the parietes (A. II).

* This vessel does not appear to be present in a female *Amphisbæna cinerea* examined by V. BEDRIAGA (9). He figures the parietal veins from this region of the body as opening directly into the efferent renal veins.

A. I. *Venæ vertebrales* (text-fig. 9).—The vertebral veins come from the region of the vertebræ. There are nine of them on the right side and eight on the left, opening into the afferent supra-renal vein, and the anterior vessels on each side are connected with the corresponding parietals.

A. II. *Venæ parietales* (text-fig. 9).—On the right side are two large parietal veins which unite with their corresponding vertebrals, and, by means of the common trunk so formed, drain into the afferent supra-renal. At their



TEXT-FIG. 11.—The Post Caval, Renal Portal, Renal Efferent and Spermatic Veins, and their connections.

Veins.—*V.A.R.*, vena anastomotica renalis; *V.C.*, vena caudalis; *V.Cl.*, vena cloacalis; *V.C.P.*, vena cava posterior; *V.I.*, vena inguinalis; *V.R.A.*, venæ renales advehentes; *V.Re.*, vena rectalis; *V.R.R.*, venæ renales revehentes; *V.Sp.D.*, vena spermatica dextra; *V.Sp.S.*, vena spermatica sinistra.

L.Kid., left kidney; *L.Lo.*, left lobe of liver; *Lt.Sup.Ren.*, left supra-renal body; *L.Tes.*, left testis; *Mesor.*, mesorchium; *Rt.Kid.*, right kidney; *Rt.Lo.*, right lobes of liver; *Rt.Lu.*, right lung; *Rt.Sup.Ren.*, right supra-renal body; *Rt.Tes.*, right testis.

distal extremity these two parietal veins open into the lateral parietal vein, so forming well marked anastomoses between it and the afferent supra-renal, placing the supra-renal portal system into communication with the system of the caudal vein. On the left side there is only one similarly constituted vein.

The next two right parietal veins are reduced, and join together before uniting with the vertebral. The parietal factors on both sides caudad of those described get so much reduced that they practically disappear.

The System of the Caudal Vein (text-fig. 11).

This system forms in the main a portal system to the kidneys, *i.e.*, most of the blood brought by it passes through the substance of the kidneys, and is returned to the heart by way of the efferent renal veins.

A. *Vena caudalis* (text-fig. 11).—The caudal vein commences far back in the tail, and runs forward in the hæmal arches, receiving paired factors from the muscle segments on its way. Just before reaching the hinder end of the kidneys it becomes swollen, receives veins from the inguinal region (A. I), and shows a tendency to split into two. Finally, it does divide into two veins, which diverge and enter the posterior ends of the kidneys, becoming the afferent renal veins (B).

A. I. *Vena inguinalis* (text-fig. 11).—The inguinal vein is a well marked vessel on each side bringing in blood from the inguinal region.

B. *Venæ renales advehentes* (text-figs. 11 and 13).—The right afferent renal or Jacobson's vein is generally smaller than the left. They both enter the posterior ends of the corresponding kidneys and run forward, partially buried in the kidney substance in its mid-ventral line. Each receives a cloacal (B. I) and a rectal factor (B. II). The vessel gradually diminishes in size, breaking up in the kidney. It sends a fair sized branch in the deep cleft between the first and second kidney lobes which turns dorsally and enters the iliac vein, thus establishing a direct connection between the systems of the caudal and abdominal veins. BEDDARD (7, p. 464) states that in *Sphenodon* he was unable to find any such connection, and opines that if the two systems are connected at all it is only indirectly through the kidney substance. The vessel, although hidden in a cleft, shows clearly in a well injected specimen, and was also found in the other specimens examined. It is a vein very similar to that figured in *Lacerta* by HOCHSTETTER (46, Plate 16, fig. 12), save that it runs in a cleft in the kidney and not superficially across its ventral surface.

B. I. *Vena cloacalis.*—The cloacal vein is a small tributary from the side of the cloaca entering the afferent renal about 6–8 mm. from the posterior end of the kidney.

B. II. *Vena rectalis.*—The rectal vein comes from the dorsum of the anal gland and receives small factors from the base of the bladder. It enters the afferent renal just anterior to the cloacal vein.

The following three systems are, strictly speaking, all parts of the one hepatic portal series of veins, since they all take blood to the liver. For convenience, however, they may be treated separately and dealt with as a main hepatic portal system with two closely related accessory systems, that of the anterior abdominal vein and that of the epigastric veins.

The Hepatic Portal System (text-figs. 10 and 12).

This system is, on the whole, similar to that in *Lacerta viridis* and figured by HOCHSTETTER (*loc. cit.*, Plate 16, fig. 15). It differs mainly in the fact that it has a large anterior gastric factor, which itself gives off a number of portal branches directly to the liver.

A. *Vena porta* or *Vena hepatica advehens* (HOCHSTETTER) (text-figs. 10 and 12).—The hepatic portal vein is quite a short trunk formed mainly by the union of the lieno-gastric (A. I) and intestinal (A. II) veins, and is distributed mainly to the right lobes of the liver, while the left lobes of the liver are supplied almost entirely by the anterior gastric factor (A. III).

A. I. *Vena gastero-lienalis* (HOCHSTETTER) (text-fig. 10).—The lieno-gastric vein is formed at the anterior end of the spleen, when a number of small factors and one larger one (A. I. β) from that body join a small gastric vein (A. I. α). It is soon joined by another small gastric tributary (A. I. γ) and runs in the mesentery alongside the pancreas, from which it receives a vessel (A. I. δ). Finally it joins the intestinal vein in the neighbourhood of the pylorus, from which part of the gut it also receives blood (A. I. ε).

A. I. α. *Vena gastrica* 1.—The first gastric vein is a small vessel arising from the left hand side of the stomach about half-way down. It runs freely in the lieno-gastric omentum, and at the anterior end of the spleen receives from that body six or eight small veins.

A. I. β. *Vena lienalis.*—The splenic vein is a trunk formed by the union of a number of small factors from the posterior end of the spleen, and after a short course it unites with the first gastric vein to form the lieno-gastric.

A. I. γ. *Vena gastrica* 2.—The second gastric vein is another small vessel coming from the caudal end of the cardiac part of the stomach and entering the lieno-gastric shortly after this leaves the spleen.

A. I. δ. *Venæ pancreaticæ.*—As the main trunk passes the pancreas a number of small tributaries from that gland flow into it.

A. I. ε. *Vena pylorica.*—The pyloric vein is constituted by the union of a number of a small branches from the region of the pylorus, and it joins the main trunk just before it enters the intestinal.

A. II. *Vena intestinalis* (text-fig. 10).—The intestinal vein commences low down on the rectum as a rectal vein, and leaving its cranial end runs forward in the mesentery to unite with the lieno-gastric. During its path through the mesentery two tributaries from the intestine (A. II. β and γ) and one from the duodenum (A. II. α) flow into it.

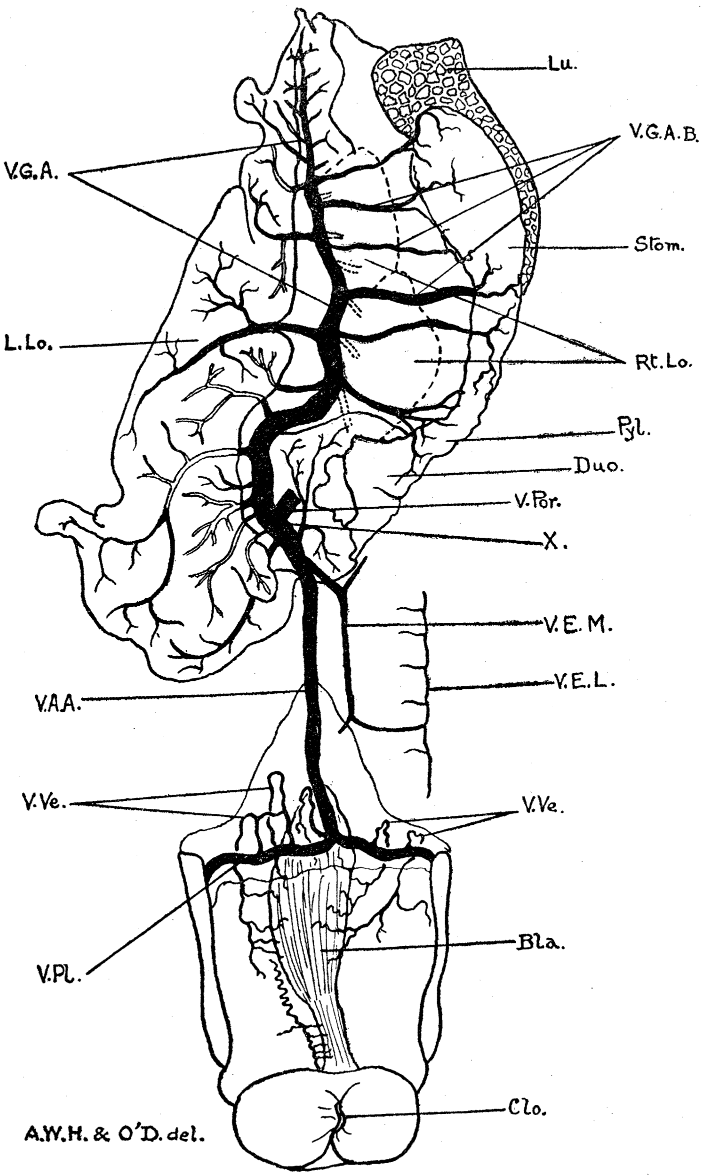
A. II. α. *Vena duodenalis.*—The duodenal vein is composed of several branches from the duodenum, which unite to form a single vessel entering the intestinal vein just before it joins the lieno-gastric.

A. II. β. *Vena intestinalis anterior.*—The front end of the intestine is drained by the anterior intestinal vein, which enters the main intestinal vein as it passes through the mesentery.

A. II. γ. *Vena intestinalis posterior.*—The posterior intestinal vein comes from the remaining and hinder part of the intestine as far back as the rectum. It reaches the main trunk a short distance caudal of the anterior intestinal vein.

A. III. *Vena gastrica anterior* (text-fig. 12).—The anterior gastric vein is a large vessel originating in the gastro-hepatic omentum near the anterior end of the stomach in a twig coming from that organ. It passes backwards close to the left lobe of the liver, receiving five or six large tributaries coming from the whole of the stomach back to the duodenum. Near the end of that lobe of the liver it bends in suddenly to enter the main hepatic portal trunk as this enters the right liver lobes. Just at the point where it turns it receives the large anterior abdominal vein (A. III. α); indeed, it appears as if it were a continuation of that vessel, as a glance at the text-figure (*i.e.*, 12) will show.

BEDDARD, indeed (7, p. 464), regards it as a forward extension of that vein, for he says: "The anterior abdominal vein, reinforced by the portal, runs in the membrane which connects the stomach with the left lobe of the liver, giving off branches to the liver substance and receiving at intervals branches from the stomach. Towards the anterior end of the liver the conjoined porto-abdominal trunk finally disappears in the liver." He instances an example of a similar distribution in a snake, *Eryx* (5), and claims *Pygopus* as showing an intermediate condition (7). In spite of its appearance, however, I think it better to regard this vessel as an anterior gastric factor of the hepatic portal system corresponding to the several gastric veins in *Lacerta viridis* according to HOCHSTETTER (2), which open separately into the liver. The vessel, moreover, is in a similar position to a corresponding gastro-hepatic factor in *Salamandra* and *Triton*, with which it is no doubt homologous. The matter can only be definitely settled, however, by reference to its development, but, of course, there must be some such portal vessel or vessels draining the



TEXT-FIG. 12.—Diagram of the Anterior Abdominal Vein, showing its relation to the Liver, the Epigastric and Hepatic-Portal Veins.

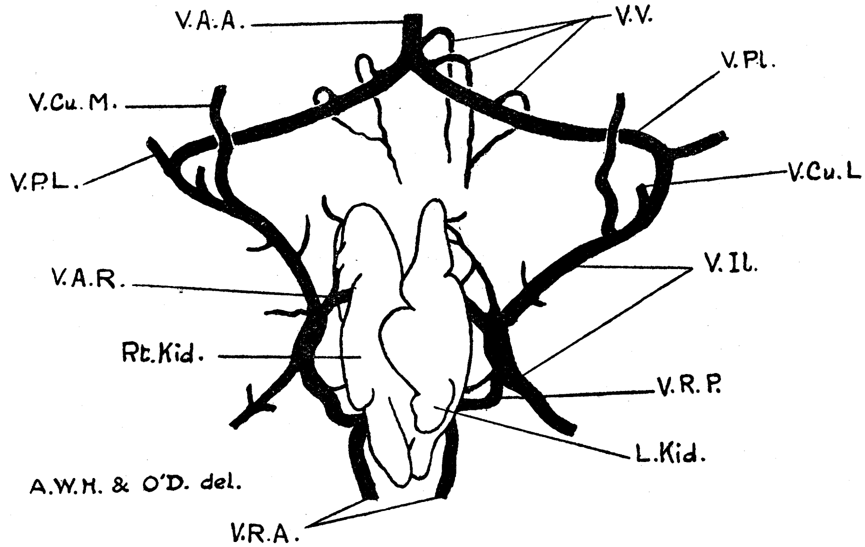
Veins.—*V.A.A.*, vena abdominalis anterior; *V.E.L.*, vena epigastrica lateralis; *V.E.M.*, vena epigastrica media; *V.G.A.*, vena gastrica anterior; *V.G.A.B.*, gastric branches of the vena gastrica anterior; *V.Pl.*, vena pelvica; *V.Por.*, vena porta; *X.*, point of entrance of the anterior abdominal vein into the anterior gastric as the latter joins the main hepatic portal trunk.

Bla., bladder; *Clo.*, cloaca; *Duo.*, duodenum; *L.Lo.*, left lobe of liver dorsal surface; *Lu.*, lung; *Pyl.*, pylorus; *Rt.Lo.*, right lobes of liver seen through mesentery; *Stom.*, stomach.

stomach before the two lateral abdominal veins have joined to form the single anterior abdominal.

All along its course it gives numerous short venæ advehentes, mostly to the left lobes of the liver, but some also to the right, so that most of its blood can go straight to the liver substance without entering the main hepatic portal trunk. Indeed, as will be seen, most of the blood from the main portal vessel goes to the right lobes, while the bulk of that from the anterior abdominal vein and the anterior gastric goes to the left lobes.

A. III. *α. Vena abdominalis anterior.*—The anterior abdominal vein, although really only a factor of the anterior gastric, is here treated separately as a matter of convenience.



TEXT-FIG. 13.—The Pelvic Ring, showing the relation of the Iliac, Renal, and Anterior Abdominal Veins. The outer edges of the kidney turned over mesially.

Veins.—*V.A.A.*, vena abdominalis anterior; *V.A.R.*, vena anastomotica renalis; *V.Cu.L.*, vena cutanea lateralis; *V.Cu.M.*, vena cutanea magna; *V.Il.*, vena iliaca communis; *V.Pl.*, vena pelvica; *V.P.L.*, vena parietalis lateralis; *V.R.A.*, venæ renales advehentes; *V.R.P.*, vena renalis posterior; *V.V.*, venæ vesicæ.

L.Kid., left kidney; *Rt.Kid.*, right kidney.

The System of the Anterior Abdominal Vein (text-figs. 12 and 13).—As has just been pointed out, the anterior abdominal vein opens into the anterior gastric branch of the hepatic portal vein, and so is portal to the liver.

Vena abdominalis anterior (HOCHSTETTER) (text-figs. 12 and 13).—The anterior abdominal vein is formed in the mid-ventral line by the union of the two pelvic veins (A), which, in their turn, are continuations of large branches from the common iliac veins (B). Its relations to the common iliac veins and to the afferent renal system is very similar to that in *Salamandra maculosa* as figured and described by HOCHSTETTER (45), and also in *Salamandra, Triton* and *Spelerpes* according to BETHGE (11). Although there seems to be a connection between the roots of the anterior abdominal and afferent renal vessels generally in Lacertilia, it varies considerably in different forms, as has been pointed out by HOCHSTETTER (46) and in BEDDARD'S useful series of papers (2–5). It is interesting to find that *Sphenodon* and *Lacerta* retain the primitive Urodele condition. Just before entering the liver it may receive the epigastric vein (C).

A. *Vena pelvica* (Wurzel der V. abdominalis, HOCHSTETTER; R. abdominalis, GAUPP) (text-figs. 12 and 13).—The pelvic veins may be considered as arising where the common iliac veins anastomose with the afferent renal system, although they are to all appearances direct continuations of the common iliac veins. They pass forward laterally, and then turn in rather sharply ventralwards to unite in the mid-ventral line and give origin to the anterior abdominal vein. During their course each receives a series of factors (A. I–VI).

A. I and II. *Venæ parietales.*—Just as the pelvic vein turns laterally it receives a couple of small factors from the posterior parietes.

A. III. *Vena cutanea magna* (BETHGE) (text-figs. 9 and 13).—The great cutaneous vein arises from the pelvic just in front of the point where this vessel crosses the femoral nerve. It pierces the muscles and passes forwards in the subcutaneous tissue of the latero-dorsal body wall to the scapular region. Here, again, as pointed out above, it leaves its subcutaneous position, and piercing the muscles, flows into the axillaris vein laterally to the azygos vein. In spite of the fact that its posterior connections are somewhat different, it is no doubt homologous with the V. cutanea magna of the Urodela *Salamandra*, *Triton*, etc., as described by BETHGE (11).

A. IV. *Vena cutanea lateralis* (text-figs. 9 and 13).—The lateral cutaneous vein is a smaller but nevertheless well marked vein coming from the skin of the lateral body wall. It joins the pelvic shortly after the great cutaneous vein.

A. V. *Vena parietalis lateralis* (Lateral abdominal, BEDDARD) (text-figs. 9 and 13).—This vein is described by BEDDARD (*loc. cit.*) in a number of Lacertilian forms and appears to be a constant factor of the pelvics, although exhibiting a varying degree of development in different species. It has been termed the lateral abdominal vein, but this term seems open to exception.

In the Elasmobranchs (59) the lateral abdominal vein is a more ventral vessel, running from the iliac forward to the subclavian vein latero-ventrally under the peritoneum on each side. According to MARSHALL (56) in the Tadpole and GOETTE in *Bombinator igneus* (35), these two lateral veins are fused to form the median anterior abdominal vein, which acquires a secondary connection with the hepatic portal system. Certain abnormal adult specimens of *Rana*, BULLER (19), WOODLAND (81), and O'DONOGHUE (57), seem to bear out this account. If, then, this description of the formation of the anterior abdominal vein be correct, the vessel now to be described is not the homologue of the lateral abdominal of the fish. The term lateral parietal seems to be suitable, since in *Sphenodon* it arises at the level of the eighth intercostal space from a parietal vein which connects it with the supra-renal portal system (*q.v.*).

It passes backwards in the angle between dorsal and ventral body wall, receiving small parietal factors from the intercostal spaces. Before entering the pelvic vein it receives two tributaries from the adjacent musculature (A. V. α and β).

A. V. α. *Vena flexoris abdominis.*—This is a moderate sized vessel, flowing into the lateral parietal vein at the level of the hinder end of the thirteenth intercostal space. It drains the flexor abdominis muscle.

A. V. β. *Vena pubo-ischio-trochanterici.*—This is a smaller vein, coming mainly from the pubo-ischio-trochanticus muscle and joining the lateral parietal vein just before it reaches the pelvic.

A. VI. *Venæ vesicæ* (text-figs. 12 and 13).—There appear to be generally five small vesicular veins, two entering each pelvic vein shortly before its union in the middle line, and the remaining one joining the base of the anterior abdominal.

B. *Vena iliaca communis* (GAUPP; V. ischiadica, HOCHSTETTER) (text-fig. 13).—Although in his second paper (46) HOCHSTETTER terms this vessel the vena ischiadica, there is no doubt it is the same vessel that in the Amphibia he calls vena iliaca (45). The latter name is preferable from the comparative point of view, since the same vessel receives this name in Elasmobranchs (59) and Amphibia (11 and 45), and one of its tributaries is the vena ischiadica of GAUPP (31), and this corresponds most nearly with the similarly named vessel in the Mammalia (*i.e.*, the former sciatic vein of the English anatomists). The common iliac vein is the main trunk draining the whole of the hind limb, after coming in from which it turns forwards and runs along for some distance parallel with the lateral wall of the kidney. It may be regarded as finishing near the front end of that organ, where it passes as a vena anastomotica (B. I), running in a cleft in the kidney into the afferent renal vein. Just at this point, as mentioned above, it gives rise to the large pelvic vein (*q.v.*), which looks like a continuation of the common iliac, but is better regarded as a tributary of it. At the hinder end of the kidney the common iliac sends a well marked tributary into the kidney substance (B. II). From this point it passes out towards the limb, receiving after a very short distance the ischiadic vein (B. III) from the deeper muscles of the external flexor side of the thigh. It now may be termed the *Vena iliaca externa* for a short way until it enters the limb as the *Vena femoralis*. It comes out on to the extensor surface of the thigh from between the ilio-femoralis and ischio-trochantericus muscles and, running mainly beneath the former, passes down to the knee, receiving three branches at its upper end (B. IV–VI). In the lower part of this course it comes to lie close to the ischiadic artery, and may now be termed the *Vena poplitea*, and a number of branches (B. VII–X) enter it just above or just below the knee. It passes on down the extensor surface of the leg between the peroneus and extensor digitorum communis longus muscles, and may be called the *Vena peronea* down to the end of the body of the latter muscle, where it gives off a branch (B. XI), and runs on to the dorsal surface of the foot as the *Vena dorsalis pedis*. This forms an *Arcus venosus*, receiving a number of veins (B. XII–XV) from the extremity of the foot.

B. I. *Vena anastomotica renalis* (text-figs. 11 and 13).—As already noted, the front end of the iliac vein forms an anastomosing vessel that runs in a deep cleft between the first and second kidney lobes, thus putting the iliac and afferent renal vessels into direct communication. Just before turning mesiad, or just before entering the kidney substance, this vessel receives a factor (B. I. α) from the anterior end of the kidney. It is hard to say which way the blood flows in this anastomosing vein without an observation on a living specimen.

B. I. α. *Vena renalis anterior*.—This is a small factor, composed of several twigs from the first kidney lobe, and, from its constitution, looks as if it were efferent from the kidney.

B. II. *Vena renalis posterior* (text-fig. 13).—The posterior renal vein leaves the iliac and runs to the hinder kidney lobes, often giving off a fine vessel to that organ, before entering it. The direction of flow in this vessel also is not apparent, although it may be afferent to the kidney. It is not improbable that the direction of flow in both this and the preceding vein may vary in correlation with the relative changes of venous pressure in the kidney, limbs, and tail.

B. III. *Vena ischiadica* (? GAUPP).—A short distance before entering the limb, the main trunk receives a tributary, which may possibly correspond with the ischiadic vein in the frog, according to GAUPP, although, as he points out, it does not accompany the similarly named nerve. This vessel was not satisfactorily followed as in the examples examined; it was either not injected or did not contain sufficient blood to render it conspicuous. It comes from the deeper muscles on the external flexor side of the limb, and apparently drains the pubo-ischio-femoralis, pubo-ischio-trochantericus externus, pubo-ischio-tibialis and pubo-tibialis muscles, and also the deeper surfaces of the ischio-tibialis posticus and extensor triceps muscles.

The main trunk is now the *Vena iliaca externa* for a short way, and then enters the limb as the *Vena femoralis* (Plate 7, fig. 4; Plate 8, fig. 6).

B. IV. *Vena cutanea* 1 (Plate 8, fig. 6).—The first cutaneous vein is a small superficial factor, joining the main trunk high up between the ileo-femoralis and ischio-trochantericus muscles.

B. V. *Ramus muscularis* 1.—This is a larger vein, joining the femoral a little below the preceding, and composed of two main factors: one from the extensor side of the ischio-tibialis muscle and one from the ischio-tibialis-posticus.

B. VI. *Ramus muscularis* 2.—The second muscular vein is about the same size as the first, and enters about half way down the thigh. It is also composed of two branches, one from the ilio-femoralis and one from the external, lower portion of the extensor triceps muscle.

Some distance below this the main trunk is called the *Vena poplitea* (Plate 7, fig. 4; Plate 8, fig. 6).

B. VII. *Ramus muscularis* 3.—This is a short muscular trunk coming from the lower posterior part of the extensor triceps muscle.

B. VIII. *Vena cutanea* 2.—The second cutaneous vein comes from the superficial tissues close to the knee, and enters the main trunk just above the joint.

B. IX. *Ramus muscularis* 4.—A fairly large muscular branch comes from between the gastrocnemius and peroneous muscles, which it drains, and joins the popliteal vein almost at the knee joint.

B. X. *Vena circumflexa genu lateralis inferior* (GAUPP) (Plate 8, fig. 6).—The circumflex vein corresponds closely with the similarly named vessel in the frog. It enters the popliteal by two short vessels, and drains the tendinous capsule of the knee and the insertion of the extensor triceps muscle.

The main trunk is now termed the *Vena peronea* (Plate 7, fig. 4; Plate 8, fig. 6).

B. XI. *Vena anastomotica arcus venosi* (Plate 8, fig. 6).—The anastomosing vein leaves the end of the peroneal, and runs downwards and mesiad, to enter the mid region of the arcus venosus, just opposite to the interdigital vein of digits three and four.

The main trunk now becomes the *Vena dorsalis pedis* (Plate 8, fig. 6).

B. XII. *Vena circumflexa tarsi* (GAUPP) (Plate 8, fig. 6).—The tarsal circumflex vein passes round over the distal extremity of the peroneus muscle on to the plantar surface of the foot, where it is probably connected with the plantar veins, although these could not be satisfactorily made out. It receives a small twig from the outer side of the fifth digit.

B. XIII. *Venæ interdigitales* (Plate 8, fig. 6).—Three well marked interdigital veins enter the arcus venosus. The first and second come from the spaces between the fourth and fifth and third and fourth digits respectively. The third is a very short trunk, formed by the union of the two veins related to the space between digits two and three and one and two.

B. XIV. *Vena præ-pollicis.*—This vein runs up the external border of the big toe.

B. XV. *Ramus muscularis* 5.—The muscular vein comes from between the distal ends of the tibialis anticus and extensor digitorum communis longus muscle. It joins with the foregoing to form the distal end of the arcus venosus.

The System of the Epigastric Veins (text-fig. 12).—Unfortunately it was not possible to make out the details of the epigastric veins, which are never easy to dissect. They were not successfully injected in any of the specimens, and they are hidden by the dense black pigmentation of the peritoneum. Certain parts of the system, however, were traced fairly satisfactorily. The epigastric veins in the Lacertilia differ very considerably from species to species, according to the observations of BEDDARD. The most common arrangement is apparently a median epigastric vein running in the mid-ventral line, such a vessel is found, for example, in *Tiliqua scincoides* (2), *Phelsuma madagascariensis* (4), *Heloderma suspectum* (8), and *Ophisaurus apus* (7). When paired or lateral epigastric veins are present their anterior and posterior connections differ so considerably that there is apparently no common arrangement. Paired epigastric veins are present in *Varanus griseus* (8), and in yet other forms, *Iguana tuberculata* (2), *Tupinambis nigropunctatus* (3), and *Chamæleon vulgaris* (4), both lateral and median epigastric veins occur.

Sphenodon possesses a well marked median and smaller lateral epigastric veins.

Vena epigastrica lateralis (text-fig. 12).—The lateral epigastric vein is a small vessel running in the ventral abdominal wall in the region of the epigastric artery. Just behind the liver it unites with its fellow in the middle line to form the median epigastric vein. The anterior and posterior connections of this vessel could not be ascertained. In the short part of its course, over which it was traced, it was found to receive several small parietal factors. In the case of *C. vulgaris* there is a somewhat similar relation between lateral and median epigastrics, for the two former unite to form the latter, only in this case it is in front of the liver.

Vena epigastrica media (text-fig. 12).—The median epigastric vein is a somewhat short but well marked vessel formed, as far as could be seen, by the union of the two factors from the lateral epigastrics, and running forward to the hinder end of the liver. Here the main part of it enters the anterior abdominal vein, just before this joins the hepatic portal, while a smaller part passes on forward in the mid-ventral line, but it could only be followed for a short distance. In *Ophisaurus apus* the median epigastric is in two portions, and the posterior part is related to the anterior abdominal vein in a manner similar to that in *Sphenodon*. When a median epigastric vein is present it is generally related to the anterior abdominal vein.

Venæ Pulmonales (text-fig. 1).

The pulmonary veins are two moderate sized thin-walled vessels running up the ventro-lateral borders of the lungs, one on each side of the body. They increase in size as they receive numerous tributaries from the substance of the lungs themselves. Leaving the anterior end of the lungs they pass dorsally to the sinus venosus, to become closely attached to its anterior border on the atrial walls. As has been pointed out previously, they open into the postero-mesial corner of the left atrium by an aperture partly hidden by a fold of the atrial wall and quite close to the inter-atrial septum.

Summary.

The heart is on the whole reptilian but of a simple unspecialised type, in which the three main arterial vessels instead of opening directly from the ventricle come off by a short common trunk, possibly a remains of the conus arteriosus.

The arterial system in general is distinctly reptilian, and while in some respects it may recall conditions in other orders of Reptilia, it most closely resembles that of certain Lacertilians, but it is undoubtedly less specialised and shows certain interesting points of similarity with that of the Urodeles.

The same general remarks also apply to the veins, which are more primitive than those of Lacertilia, although they approximate more nearly to the latter than to other Reptiles.

Certain special points in the blood vessels will be summarised below when considering the light they throw upon the position of *Sphenodon* in the class Reptilia. It only remains to note that the blood vascular system of the Tuatara is of considerable anatomical interest, since looked at broadly it is much more primitive than that of any other Reptile so far described. On the one hand, it has resemblances to the Crocodilia, Chelonia, particularly the Lacertilia, and even the Ophidia, while on the other hand it recalls in a number of striking features that characteristic of the Urodela. In it then we have an arrangement that should be borne in mind when dealing with other forms, and one that is essential to a proper appreciation of the disposition of the vessels in the Lacertilia.

Conclusions.

As was pointed out in the introduction, two views are commonly held with regard to the systematic position of *Sphenodon*. The more common and perhaps more orthodox view, since it is the one put forward in most text-books, is that *Sphenodon* is the sole modern representative of an order of the Reptilia termed the Rhynchocephalia, equal in rank to the other four orders of the class. This suggestion was first put forward by Günther (41) in 1867. As far as palæontological records show, the order is ancient but was never an extensive one. On this ground there is no inherent improbability in its only remnant being found in Australasia, since this region has furnished other examples of orders of animals either poorly represented or not represented at all in other parts of the world. The second view put forward by HUXLEY, among others, is that the differences between *Sphenodon* and some of the least specialised Lacertilia are not so great as to justify placing it in a separate order, but, on the contrary, it should be included in the Lacertilia. It is not intended in the present paper to discuss fully all the evidence for and against these two views, but at the same time, in the course of comparing the blood vessels with those of a number of other Reptiles, it was inevitable that some attention had to be paid to evidence put forward by various writers as to the systematic position of the animal.

A full enumeration of the characteristic features of *Sphenodon* and discussions as to their value will be found in the works of BOULENGER (16), BUSCH, GADOW and HOWES and SWINNERTON, and they need not be repeated here. One or two points have been raised subsequently and call for brief notice.

GADOW (29) pointed out that *Sphenodon* lacks distinct copulatory organs, and so is to be regarded as a primitive type, and he even pointed out similarities between the cloaca in this form and in the Gymniophiona. Later, OSAWA (63) sought to homologise the cloacal scent glands with the copulatory organs of other Reptiles, and concludes (p. 346), ". . . muss ich mit der Behauptung auftreten, dass der *Hatteria* auch ein Begattungsorgan zukommt." The impossibility of homologising the scent glands with copulatory organs, for both may occur together in Snakes, was subsequently reaffirmed by GADOW, who concluded (30, p. 43): "*Hatteria* ist und bleibt das niederste lebende Reptil welches wir kennen; es gehört weder zu den Krokodilen, was niemand behaupten wird, noch zu den Saurien, . . ."

Another of these features is the characteristic forward extension of the pterygoid bones to meet the vomers, so that the palatines are, as it were, pushed to the side and excluded from participation in the formation of the middle portion of the bony palate. This, as HOWES and SWINNERTON point out, is "a feature already recognisable among the Batrachia and Stegocephalia." BEDDARD (6) afterwards described the skull of *Uromastix spinipes*, in which the pterygoids pass forwards almost, if not actually, to touch the vomers, and so called attention to the fact that this character, supposed to be peculiar to "Hatteria," is also found in a Lacertilian. This condition is very unusual in the Lacertilia; indeed, it does not appear to be found in any other species that has been described, not even in the closely allied *Uromastix hardwickii*, according to BUSCH (20). It cannot therefore be urged as showing any relationship between *Sphenodon* and the Lacertilia, for it is distinctly atypical of that order, but is better regarded as (so far as known) an isolated example of a species of Lizard that has retained a Batrachian condition that is also found in *Sphenodon* in a more complete form.

We are here more concerned with the blood vascular system than with other anatomical features, and it will simplify matters if we glance briefly at the points that have come to light in comparing *Sphenodon* with other forms. In other

Reptilia the three main arterial trunks come off separately from the ventricle, while in the Tuatara they come off from a short common trunk, probably representing the conus arteriosus of the Amphibia which has been lost in other Reptilia.

Sphenodon possesses both a ductus caroticus and a ductus arteriosus (BOTALLI) on each side, and they are in a moderately developed condition. That this is a primitive condition is shown by the fact that it occurs in the Amphibia Urodela, and is not found, so far as is known, in any other reptile. The carotids, in origin and general distribution, and also in the absence of a common trunk, *i.e.*, a carotis primaria, resemble those of the Urodele Amphibia, and also some of the primitive Lacertilia. The same is also true of the arteria laryngeo-trachealis, which comes off from the pulmonary artery in Amphibia and in certain Lizards. This vessel appears to be homologous with the arteria œsophagea of the Urodeles, and so is a relic of the time when respiration took place in the mucous membrane of the buccal cavity and pharynx. VAN BEMMELEN (10, p. 102) gives his opinion of the neck region as follows: "Vor allem stellte es sich heraus, dass *Hatteria*, im Baue ihrer Halsgegend eine typische Eidechse ist, und darin besonders mit den Ascalaboten sehr übereinstimmt." As was noted previously, he was mainly concerned with the nerves. DENDY (22) gives a comparison between the intra-cranial arteries of *Sphenodon* and other reptiles. He notes several points of difference from the Lacertilia, but, nevertheless, records the general impression (p. 411) that "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."

In regard to the gut arteries, HOCHSTETTER, in his comparative account of these vessels in Saurians, says (44, p. 217): "Dabei werde ich von *Hatteria* ausgehen, weil bei dieser Form entschieden die ursprünglichsten Verhältnisse bei *Lacerta* von denen bei *Hatteria* in einfacher Weise ableiten lassen." The same conclusion is put forward by GEGENBAUR (33, footnote, p. 536).

The arteria interossea leaves the extensor surface of the fore foot and passes through between the ends of the radius and ulna on to the flexor surface. It returns again, passing through the wrist between the carpal bones. This rather striking course is also primitive, since it is met with in the Amphibia.

Certain points in the relationships of the veins also deserve consideration. The paired venæ tracheales are in a more primitive condition than in *Lacerta*, and, indeed, represent a stage that is actually passed through by *Lacerta* in the course of its development. In all probability they are homologous with the venæ pharyngeæ in Urodele Amphibia. The vena cerebralis posterior in *Sphenodon* leaves the cranium by the foramen jugulare in company with the tenth cranial nerve, a very important point, as this vein is more or less constant in position throughout the vertebrate series. It accompanies the vagus nerve in Elasmobranchs, Urodele and Anurous Amphibia, Birds and Mammals, so that it must be regarded as primitive and fairly constant. In Lacertilia, and, as far as is known, Ophidia, this vessel leaves the cranium through the foramen magnum, and is thus separated from the vagus. This, then, is a significant difference between *Sphenodon* and the Lacertilia. The vena cerebralis media and the vena capitis dorsalis are both to be regarded as primitive, since they characterise the primitive Amphibia and Reptilia. DENDY (22) has noted several points which, in my opinion, constitute considerable differences between the intra-cranial veins of *Sphenodon* and the Lacertilia, and points out (p. 423) that "a very characteristic feature of *Sphenodon* is the development of large transverse sinuses resembling those of the Crocodile, but these communicate with the extra-cranial vascular system in quite a different manner from that described by RATHKE in the latter animal." There is present a sinus orbito-nasalis, corresponding with a vein of the same name in the Amphibia and Elasmobranchs, and this is not found in *Lacerta* or *Tropidonotus*.

In *Sphenodon* the state of development of the vena azygos and the supra-renal portal system, and also the relations of these vessels, which are remnants of the embryonic posterior cardinal vein, are more primitive than in *Lacerta*, and indeed present a condition from which any of the arrangements met with in the Lacertilia can be derived. The anterior gastric vein resembles that of the Urodele Amphibia, and although present in an Ophidian *Eryx*, does not appear to have been described in Lacertilians. The constitution of the anterior abdominal vein, while resembling that in *Lacerta* to a certain extent, and also the Urodela, is more primitive than in any member of the order to which the former belongs. BEDDARD, as the result of his work on the body veins of *Sphenodon*, concludes (7, p. 462) :—" There is no question that, apart from details, the venous system of *Hatteria* is distinctly Lacertilian. Nor do the differences which it shows from the Lacertilia tend to prove a nearer resemblance to the Chelonia or to the Crocodilia. On the other hand, I believe it possible to detect likenesses to the Ophidia. This, however, in my opinion, does not argue a special affinity between *Hatteria* and the Ophidia, but the antiquity of the *Hatteria* type which Palæontology, as is well known, has proved." Notwithstanding this view of one who has a very extensive knowledge of the blood vessels in the Reptilia, it seems to me that, when a more extended survey is taken and the many points of similarity between the vessels of *Sphenodon* and the Amphibia, especially the Urodela, are borne in mind, the above conclusions hardly go far enough, and that the primitiveness of *Sphenodon* is considerably more pronounced than they appear to indicate.

Thus, I think, it will be seen that in a large number of points, some of considerable importance, the vascular system of the Tuatara is more primitive than that in any of the Lacertilia. Indeed, if we consider the cumulative effect of all these points, it seems inevitable that we must regard the vascular system as a whole as being of a much less specialised type, so much so that it merits the placing of the animal in a separate order. Certain features need re-emphasising, the unspecialised condition of the heart, the retention of the ductus caroticus and arteriosus, and the position of the posterior cerebral vein. In this last matter, *Sphenodon* resembles both the higher and lower Vertebrates, while the Lacertilia have departed from this condition. Also, there does not appear to be any primitive condition in the vessels of any Lacertilian that is not also found in *Sphenodon;* and yet, again, in its intra-cranial vessels it gives a suggestion of the conditions realised in the Chelonia and the Crocodilia, which is just what might be expected of a primitive form.

The fact that *Sphenodon* resembles the Lacertilia in certain respects, not alone in the blood vessels, as BEDDARD has pointed out, does not, I submit, justify its inclusion in this order any more than its likenesses to the Urodela, which are many, demand its being placed with them. Indeed, the fact that *Sphenodon* has structures to be found in various Lacertilians, but not all in the same species, or even in the same genus, seems to suggest, and rather forcibly too, that when such characters are encountered in one of the Lacertilia it indicates that, in this particular respect, the Lizard has retained a primitive condition which is present in the Tuatara, and that the latter animal is more primitive than any of them. The Lacertilia differ among themselves in the disposition of their blood vessels, but when they do it is the result of modification or specialisation; whereas practically always when *Sphenodon* differs from them it will be found to be in a way that either suggests conditions in other Reptiles or most frequently approximates it more nearly to the Urodela.

The object of the present investigation was in the first place to give a fairly complete account of the blood vascular system of the Tuatara, as, owing to its rarity, an opportunity of examining a well preserved series of specimens might not occur again. Secondly, no such complete account is available for any Lacertilian, and as a large amount of comparative work has been done on various points in different species of Reptiles, it seemed desirable to correlate this with such an admittedly little specialised type to form a basis for future comparative work.

At the outset I was inclined to regard *Sphenodon* as in all probability a lowly member of the order Lacertilia. The condition of its vascular system, briefly epitomised above, however, was found to be so primitive in all respects, and to differ so much from that in the Lacertilia in certain important features, that it was obvious that it could not be included in that order. Reference to the somewhat extensive literature regarding other points in its anatomy disclosed no valid reason that would necessitate its being placed among the Lacertilia; but, on the other hand, it brought out a number of points (more than need be dealt with here) to show it to be a more primitive type of Reptile. I have therefore been led to conclude that while *Sphenodon* approaches the Lacertilia more closely than any other order of the Reptilia, it nevertheless differs from them to such an extent that GÜNTHER was thoroughly justified in placing it in a separate order, the Rhynchocephalia, and that it is the most primitive living Reptile.

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DESCRIPTION OF PLATES.

PLATE 6.

Fig. 1.—Diagrammatic sketch of a general view of the viscera of Sphenodon, with the alimentary canal displaced to the right.

Vessels.

A.C., arteria cœliaca; *A.E.A.*, arteria epigastrica anterior; *A.I.C.*, arteria iliaca communis; *A.Il.E.*, arteria iliaca externa; *A.L.*, arteria lumbalis; *A.M.C.*, arteria mesenterica communis; *A.S.*, arteria scapularis; *C.E.*, carotis externa; *C.I.*, carotis interna; *D.Ao.*, dorsal aorta; *R.E.A.* 1, ramus muscularis of arteria epigastrica; *V.*, ventricle; *V.A.A.*, vena abdominalis anterior; *V.Az.*, vena azygos; *V.C.A.S.*, vena cava anterior sinistra; *V.Co.C.*, vena coraco-clavicularis; *V.C.P.*, vena cava posterior; *V.Cu.L.*, vena cutanea lateralis; *V.Cu.M.*, Vena cutanea magna; *V.Il.*, vena iliaca communis; *V.J.E.*, vena jugularis externa; *V.J.I.*, vena jugularis interna; *V.Pl.*, vena parietalis lateralis; *V.R.R.*, venæ renales revehentes; *V.Sc.*, vena subclavia; *V.Sp.D.*, vena spermatica dextra; *V.Sp.S.*, vena spermatica sinistra; *V.Ve.*, venæ vesicæ.

Other Structures.

Blad., bladder; *G.Blad.*, gall bladder; *Int.*, intestine; *Liv.*, liver; *Mesor.*, mesorchium; *Rect.*, rectum; *Rib.*, cut end of ribs; *Rt.Kid.*, right kidney; *Rt.Lung*, right lung; *Rt.Tes.*, right testis.

PLATE 7.

Fig. 2.—Diagrammatic sketch of the vessels shown in a lateral dissection of the head, certain of the bones having been removed.

Vessels.

A.A., arteria articularis; *A.Au.*, arteria auricularis; *A.F.*, arteria frontalis; *A.Mn.*, arteria mandibularis; *A.M.G.*, arteria musculo-glandaris; *A.Mn.E.*, arteria mandibularis externa; *A.Mn.I.*, arteria mandibularis interna; *A.N.*, arteria nasalis; *A.Oc.*, arteria occipitalis; *A.O.I.*, arteria orbitalis inferior; *A.Op.*, arteria ophthalmica; *A.O.S.*, arteria orbitalis superior; *A.T.*, arteria temporalis; *R.C.*, ramus coronoideus; *R.C.I.*, 1 and 2, rami musculares of arteria temporalis; *R.Mn.* 1, 2 and 3, rami musculares of arteria mandibularis; *R.m.n.*, ramus membranæ nictitantis; *R.t.m.*, ramus temporo-masseteris; *S.M.N.*, sinus membranæ nictitans; *S.O.*, sinus orbitalis; *V.Ca.L.*, vena capitis lateralis; *V.Ce.M.*, vena cerebralis media; *V.Ce.P.*, vena cerebralis posterior; *V.Ce.R.*, ramus muscularis of vena cerebralis posterior; *V.J.I.*, vena jugularis interna; *V.J.R.* 2–6, rami musculares of vena jugularis interna; *V.Mn.*, vena mandibularis; *V.Mn.I.*, vena mandibularis interna; *V.Mn.R.*, rami musculares of vena mandibularis; *V.Oc.*, vena occipitalis; *V.Pt.*, vena pterygoidea; *V.S.*, vena supra-temporalis; *V.T.A.*, vena tympanica anterior; *V.T.A.R.*, ramus muscularis of vena tympanica anterior.

Other Structures.

1, cleido-humeralis muscle; 2, ventral part of levator scapulæ; 3, dorsal part of levator scapulæ; 4, longissimus; 5, cucullaris; 6, cut end of parietal bone; 7, parietal bone; 8, columella cranii; 9, cut end of post-frontal bone; 10, rectus superior; 11, frontal bone; 12, obliquus superior; 13, Harderian gland; 14, obliquus inferior; 15, rectus inferior; 16, cut end of jugal bone; 17, coronoid process of mandible; 18, cut end of quadrato-jugal bone; 19, cut end of squamosal and quadrate bones; 20, anterior hyoid bone; 21, posterior hyoid bone; *V*, nervus trigeminus; *X*, vagus.

Fig. 3.—Diagrammatic sketch of the arteries and veins shown in a dissection of the head and neck from the ventral side.

Vessels.

A.Gg., arteria genio-glossa ; *A.Gp.*, arteria glossopharyngeus ; *A.L.T.*, arteria laryngeo-trachealis ; *A.M.*, arteria muscularis cervicis ; *A.Oe.*, arteria œsophagea ; *A.P.S.*, arteria pterygoideus superficialis ; *A.S.M.*, arteria submandibularis ; *A.T.I.*, arteria thyreoidea inferior ; *A.T.S.*, arteria thyreoidea superior ; *C.C.*, carotis communis ; *C.E.*, carotis externa ; *C.I.*, carotis interna ; *D.C.*, ductus caroticus ; *L.S.A.*, left systemic arch ; *R.m.m.*, ramus musculo-mandibularis ; *S.A.*, systemic arch ; *V.C.A.D.*, vena cava anterior dextra ; *V.J.C.D.*, vena jugularis communis dextra ; *V.J.C.S.*, vena jugularis communis sinistra ; *V.J.E.*, vena jugularis externa ; *V.J.I.*, vena jugularis interna ; *V.J.R.* 1–5, rami musculares of vena jugulares ; *V.O.*, venæ œsophageæ ; *V.Sc.*, vena subclavia ; *V.T.R.I.*, ramus muscularis of vena trachealis.

Other Structures.

Cer.Sym., cervical sympathetic ; *Gen.gl.*, genio-glossus ; *Gen.hy.*, genio-hyoid ; *Hy.* 1, anterior cornu of hyoid ; *Hy.* 2, posterior cornu of hyoid ; *Hyo-man.*, hyo-mandibularis ; *Int.Pte.*, internal pterygoid ; *Lev.Hy.*, levator hyoidens ; *Plat.*, platysma ; *Rec.Lar.X.*, recurrent laryngeal of vagus ; *Tra.*, trachea ; X., vagus ; XII., hypoglossal.

PLATE 8.

Figs. 4–10, Diagrammatic Sketches—

Fig. 4.—Vessels of the left hind limb viewed from the extensor surface.

Fig. 5.—Deeper arteries of the right hind foot viewed from the flexor (plantar) side.

Fig. 6.—Veins of the right hind limb viewed from the extensor surface.

Fig. 7.—Veins of the right fore limb viewed from the extensor surface.

Fig. 8.—Vessels of the left fore limb viewed from the extensor surface.

Fig. 9.—Vessels of the left fore limb viewed from the flexor surface.

Fig. 10.—Relation of the arteries to the muscles of the eye viewed from the inner aspect.

Muscles of Hind Limb.

5, ileo-femoralis ; 9, ischio-trochantericus ; 11, ischio-tibialis posticus ; 13, ilio-fibularis ; 14, extensor triceps ; 15, gastrocnemius ; 16, flexor digitorum communis profundus ; 17 and 20, tibialis anticus ; 21, extensor digitorum communis longus ; 22, peroneus ; 23, abductor et extensor hallucis longus ; 29, abductor digitorum communis ; 32, interossei planteres.

Arteries of Hind Limb.

A.C.F.E., arteria circumflexa femoris externa ; *A.C.F.I.*, arteria circumflexa femoris interna ; *A.C.G.E.*, arteria circumflexa genu externa ; *A.C.G.I.*, arteria circumflexa genu interna ; *A.D.P.*, arteria dorsalis pedis ; *A.I.*, arteriæ interdigitales ; *A.I.E.*, arteria interossea externa ; *A.Io.*, arteria interossea ; *A.Is.*, arteria ischiadica ; *A.M.E.*, arteria metatarsalis externa ; *A.M.I.*, arteria metatarsalis interna ; *A.P.P.*, arteria perforans plantaris ; *A.T.L.*, arteria tibialis lateralis ; *A.T.M.*, arteria tibialis media ; *R.I.C.* 1 and 2, rami musculares 1 and 2 of the arteria iliaca communis.

Veins of Hind Limb.

V.A.V., vena anastomotica arcus venosi ; *V.C.G.*, vena circumflexa genu lateralis inferior ; *V.C.T.*, vena circumflexa tarsi ; *V.Cu.* 1 and 2, venæ cutaneæ ; *V.D.P.*, vena dorsalis pedis ; *V.D.R.* 5, ramus muscularis of the vena dorsalis pedis ; *V.F.*, vena femoralis ; *V.F.R.* 1 and 2, rami musculares of the vena femoralis ; *V.I.*, venæ interdigitales ; *V.Pe.*, vena peronea ; *V.Po.*, vena poplitea ; *V.Po.R.* 4, ramus muscularis of the vena poplitea ; *V.P.P.*, vena præ-pollicis.

I Pollex ; II–V digits (figs. 4–6).

Muscles of Fore Limb.

2, latissimus dorsi ; 11, pectoralis ; 12, cleido-humeralis ; 13, dorsalis scapulæ ; 14, supra-coracoideus ; 15, coraco-brachialis ; 17, scapulo-humeralis posterior ; 18, scapulo-coraco-brachialis ; 19, coraco-antibrachialis ; 22, anconæus ; 23, flexor-carpi-radialis ; 24, flexor-digitorum-communis-profundus ; 26, pronator teres ; 27, pronator quadratus ; 28, supinator ; 29, extensor carpi radialis brevis ; 30, extensor digitorum communis longus ; 31, extensor carpi ulnaris ; 32, anconæus quartus (richtiger quintus) ; 33, extensor carpi radialis longus ; 34, abductor et extensor pollicis longus ; 35, flexor digitorum communis sublimis ; 43, extensor digitorum communis brevis.

Arteries of Fore Limb.

A.B., arteria bicipitalis ; *A.I.*, arteriæ interdigitales ; *A.I.E.*, arteria interossia externa ; *A.Io.*, arteria interossea ; *A.U.*, arteria ulnaris ; *A.V.*, arteria volaris ; *A.V.P.*, arcus volaris profundus ; *R.r.*, ramus radialis ; *Rr.* 1, ramus radialis of arcus dorsalis ; *Ru.*, ramus ulnaris ; *Ru.* 1, ramus ulnaris of arcus dorsalis.

Veins of Fore Limb.

A.V.D., arcus venosus dorsi manus; *V.A.L.*, vena anastomatica longa; *V.A.S.*, vena antibrachialis superficialis; *V.A.V.*, vena anastomatica arcus venosi; *V.B.*, vena branchialis; *V.B.R.*, *V.B.R.* 2, rami musculares of vena brachialis; *V.Cu.M.*, vena cutanea magna; *V.I.*, vena interdigitales; *V.Io.*, vena interossea; *V.P.B.*, vena profunda brachii; *V.P.H.*, vena præ-hallucis.

Sketch of Dissection of Eye from inner aspect (fig. 10).

Arteries.

A.F., arteria frontalis; *A.M.G.*, arteria musculo-glandaris; *A.N.*, arteria nasalis; *A.Op.*, arteria ophthalmica; *A.O.S.*, Arteria orbitalis superior; *C.* 1, branch to posterior rectus; *C.* 3, branch to superior rectus; *C.* 4, branch to back of eye; *C.* 5, branch to anterior rectus; *C.* 6, branch to inferior rectus.

Muscles.

Rect.Ant., rectus anterior; *Rect.Inf.*, rectus inferior; *Rect.Post.*, rectus posterior; *Rect.Sup.*, rectus superior; *Ret.Bul.*, retractor bulbi; *Obl.Inf.*, obliquus inferior; *Obl.Sup.*, obliquus superior; *Hard.Gl.*, Harderian gland; *II.*, optic nerve.

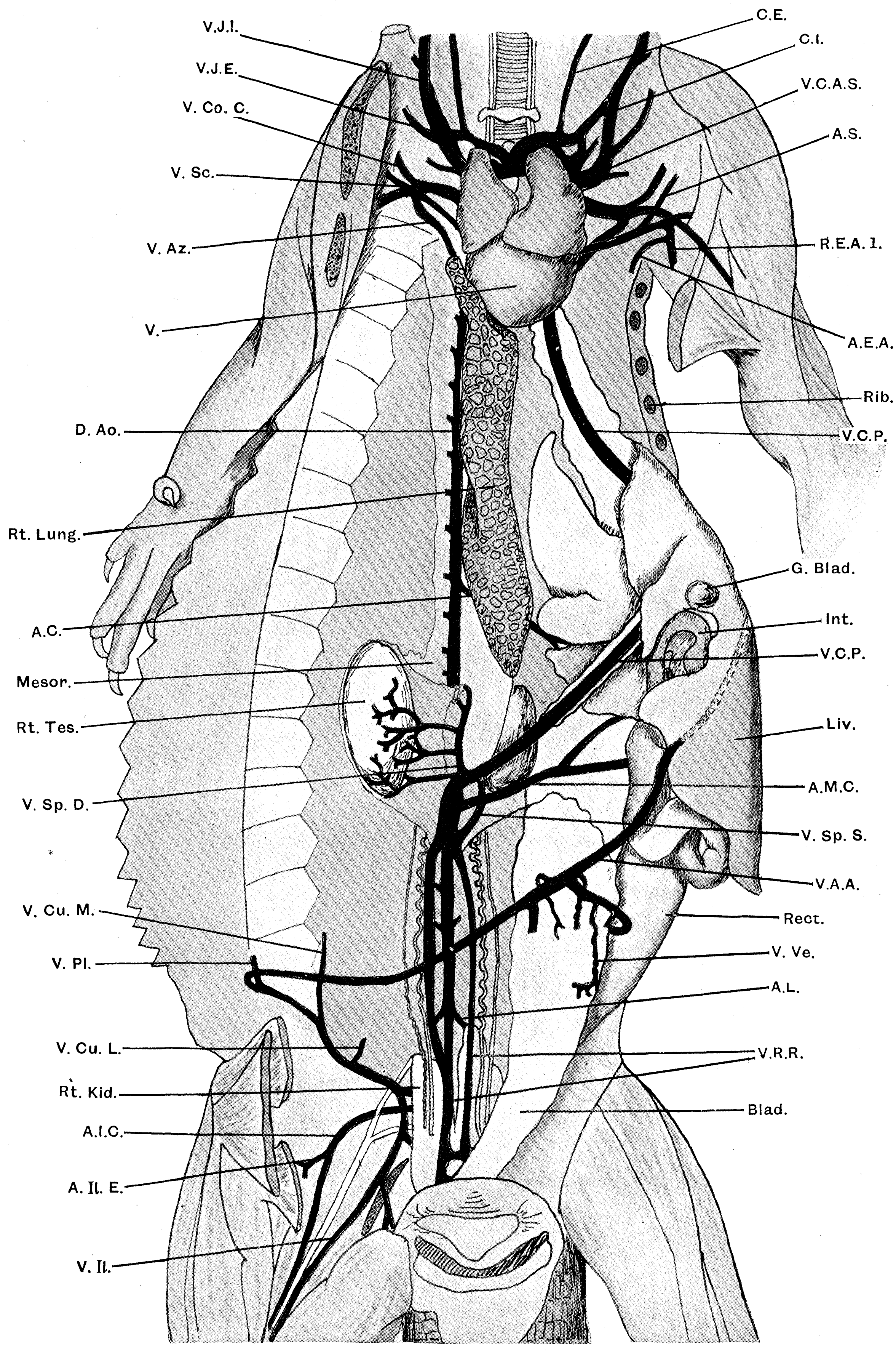
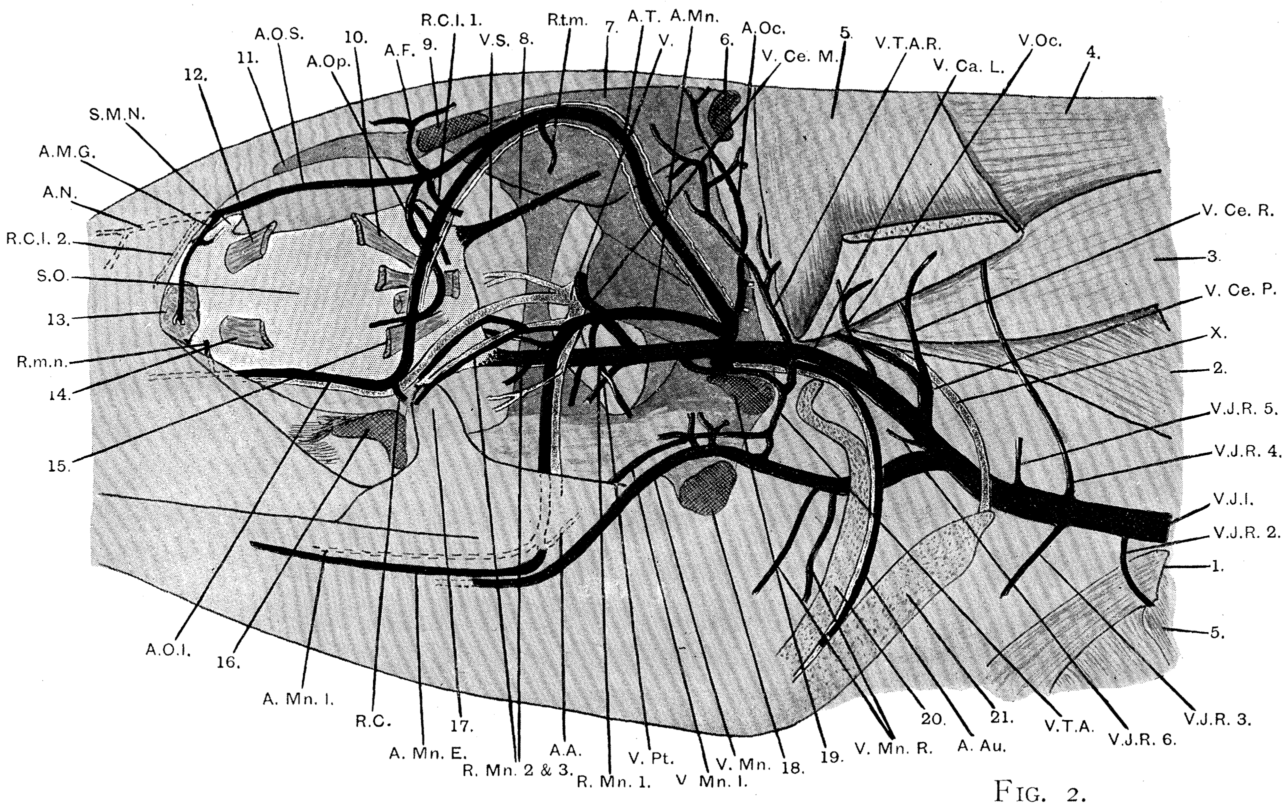
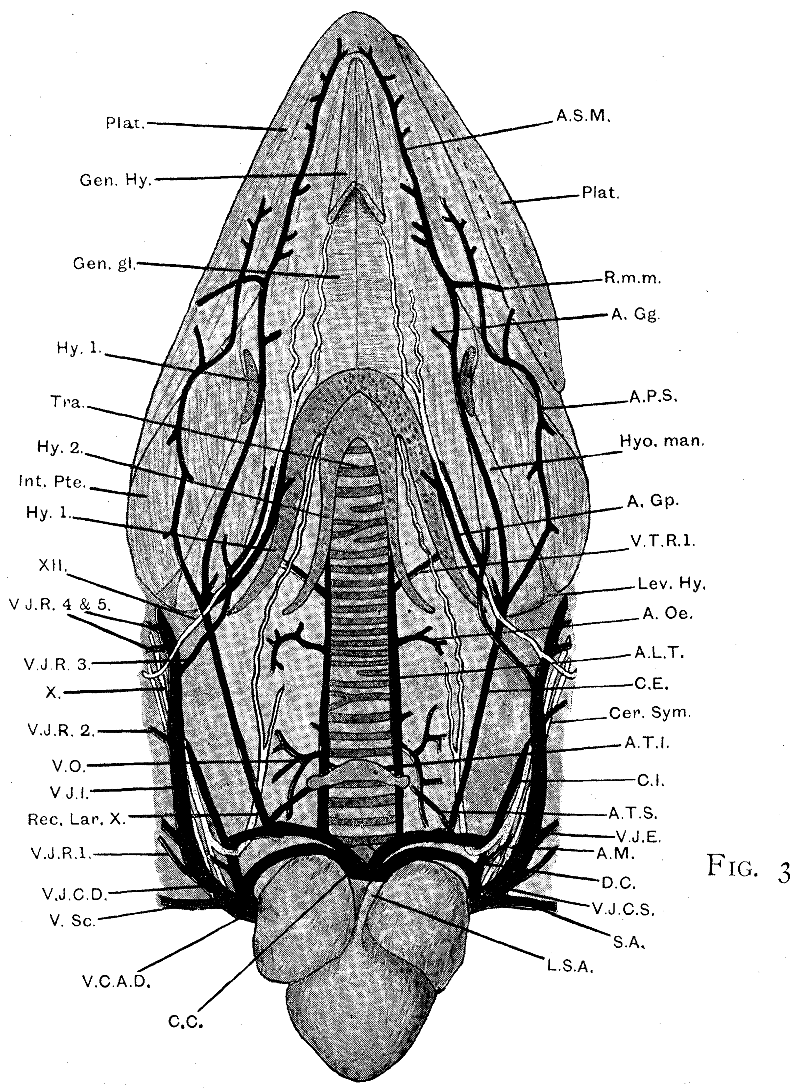

V.J.I.
V.J.E.
V. Co. C.
V. Sc.
V. Az.
V.
D. Ao.
Rt. Lung.
A.C.
Mesor.
Rt. Tes.
V. Sp. D.
V. Cu. M.
V. Pl.
V. Cu. L.
Rt. Kid.
A.I.C.
A. Il. E.
V. Il.
C.E.
C.I.
V.C.A.S.
A.S.
R.E.A. 1.
A.E.A.
Rib.
V.C.P.
G. Blad.
Int.
V.C.P.
Liv.
A.M.C.
V. Sp. S.
V.A.A.
Rect.
V. Ve.
A.L.
V.R.R.
Blad.

Fig. 1.



R.C.I. 1.
A.T.
A.Mn.
A.O.S.
10.
Rtm.
7.
A.Oc.
5.
V.Oc.
11.
A.F.
9.
V.S.
8.
V.
6.
V.T.A.R.
4.
12.
A.Op.
V. Ce. M.
V. Ca. L.
S.M.N.
A.M.G.
A.N.
V. Ce. R.
R.C.I. 2.
3.
S.O.
V. Ce. P.
13.
X.
R.m.n.
2.
14.
V.J.R. 5.
15.
V.J.R. 4.
V.J.I.
V.J.R. 2.
1.
5.
A.O.I.
16.
A. Mn. I.
R.C.
17.
20.
21.
V.T.A.
V.J.R. 3.
A. Mn. E.
A.A.
V. Pt.
V. Mn.
18.
19.
V. Mn. R.
A. Au.
V.J.R. 6.
R. Mn. 2 & 3.
R. Mn. 1.
V Mn. I.

FIG. 2.



Plat.
A.S.M.
Gen. Hy.
Plat.
Gen. gl.
R.m.m.
A. Gg.
Hy. 1.
A.P.S.
Tra.
Hyo. man.
Hy. 2.
Int. Pte.
A. Gp.
Hy. 1.
V.T.R.1.
XII.
Lev. Hy.
V J.R. 4 & 5.
A. Oe.
V.J.R. 3.
A.L.T.
X.
C.E.
Cer. Sym.
V.J.R. 2.
A.T.I.
V.O.
C.I.
V.J.I.
Rec. Lar. X.
A.T.S.
V.J.E.
V.J.R.1.
A.M.
D.C.
V.J.C.D.
V.J.C.S.
V. Sc.
S.A.
L.S.A.
V.C.A.D.
C.C.

FIG. 3.

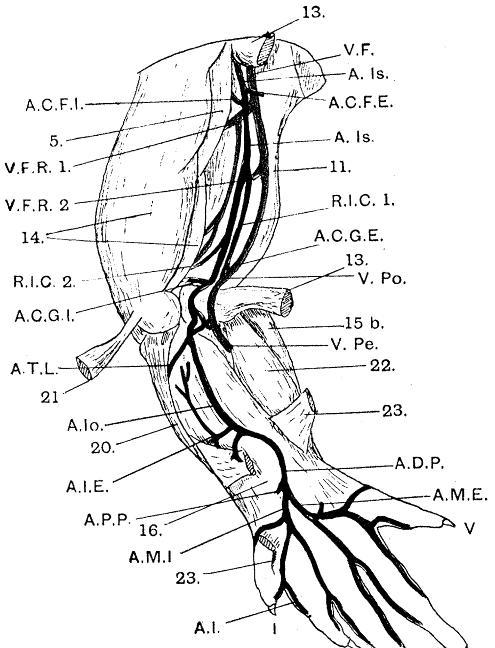


FIG. 4.

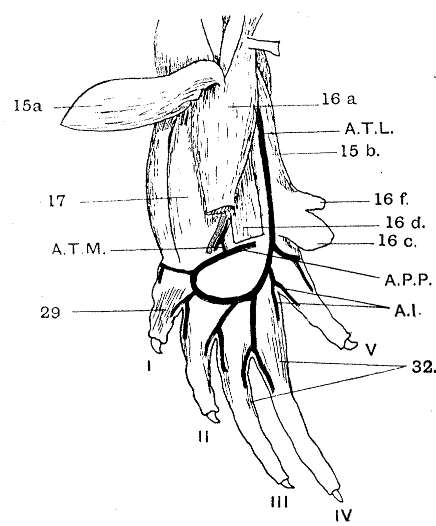


FIG. 5.

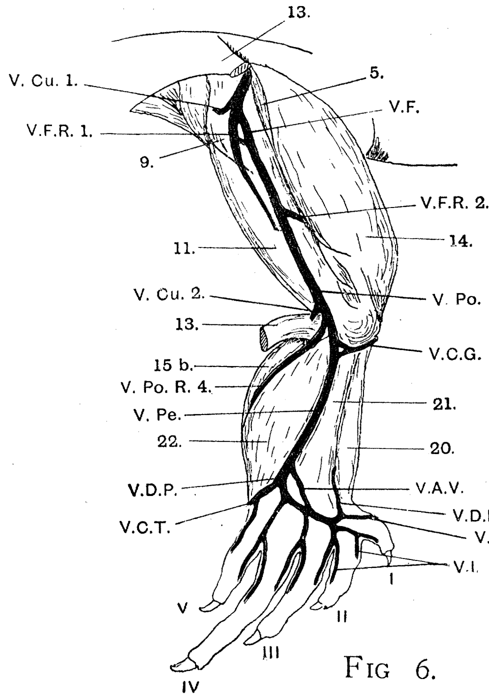


FIG 6.

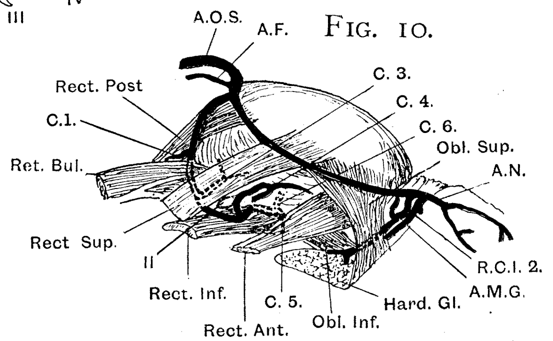


FIG. 10.

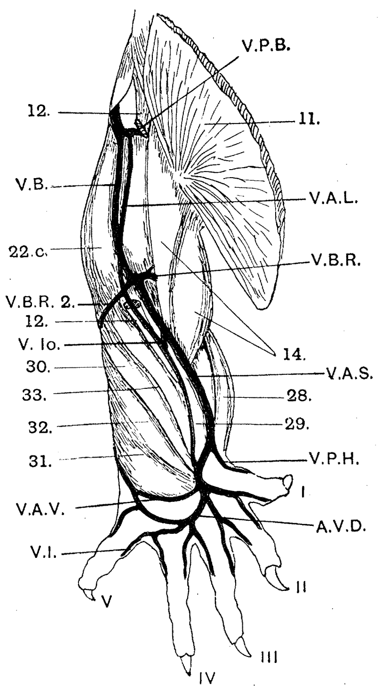


FIG. 7.

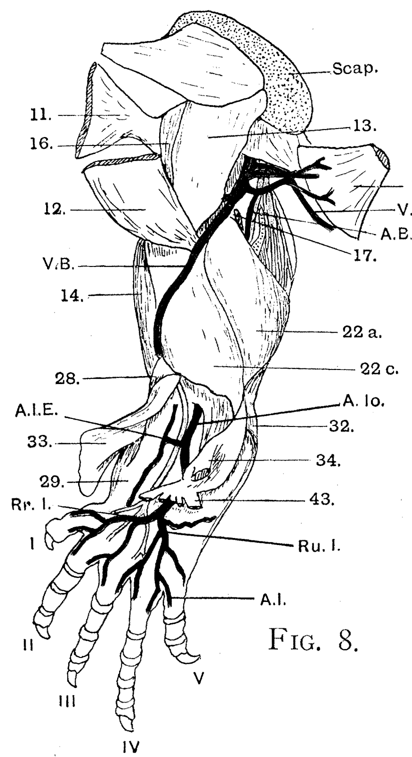


FIG. 8.

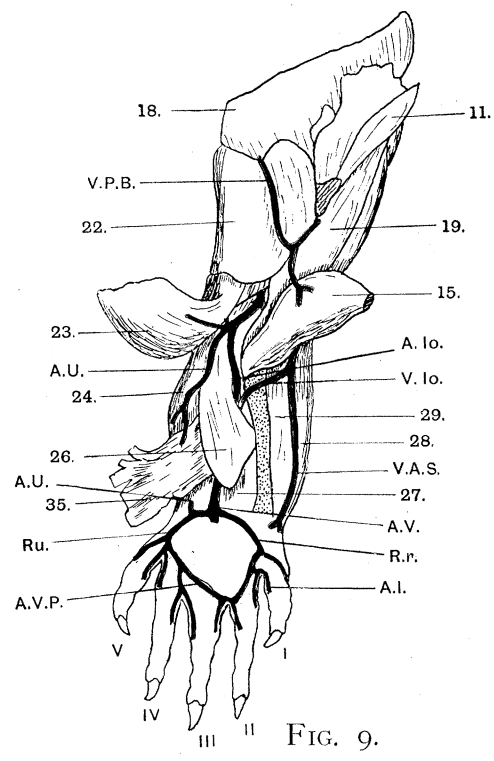
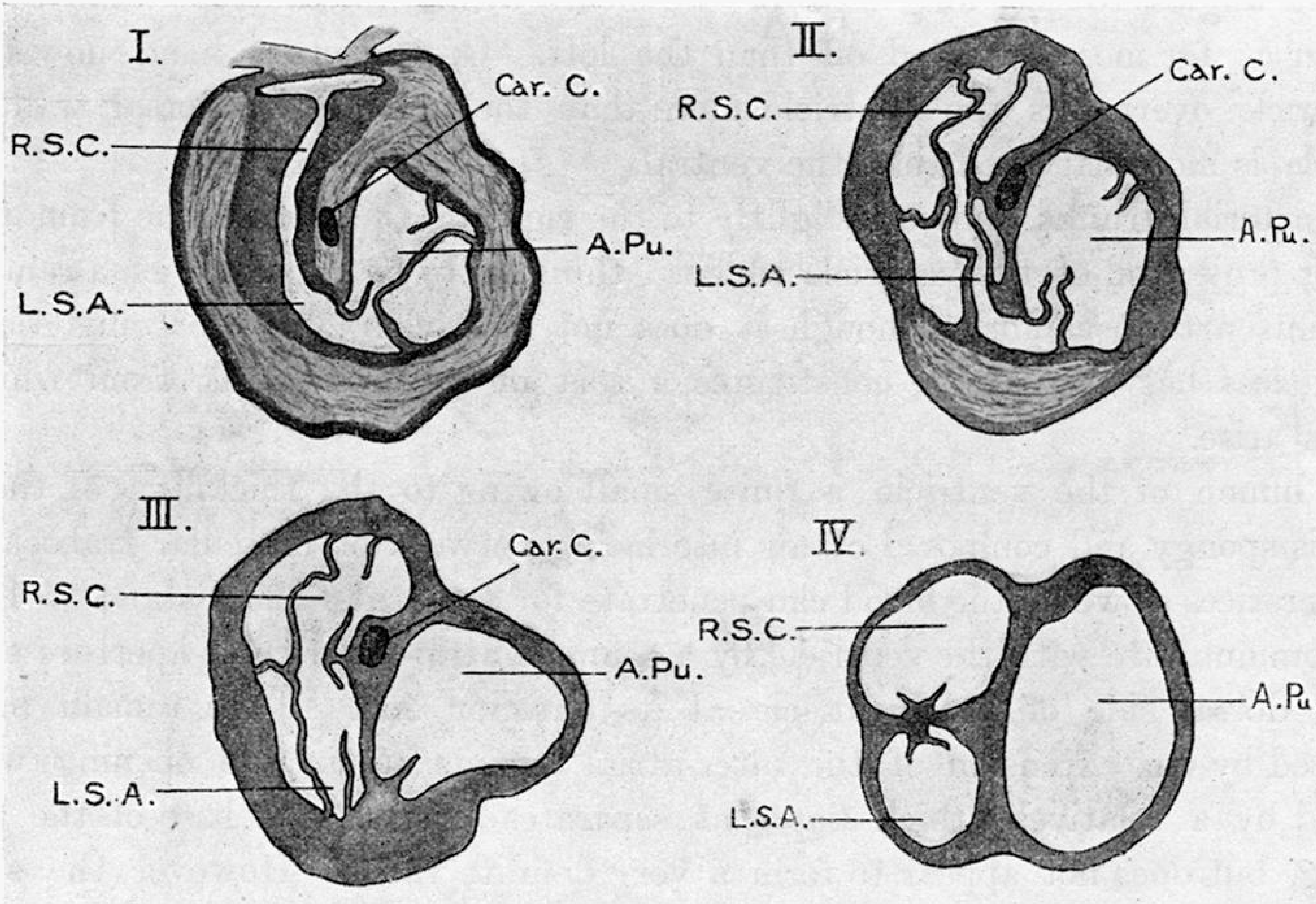


FIG. 9.



TEXT-FIG. 2.—Outline sketches of four sections through the Main Arterial Trunks, drawn with a Zeiss Meyer camera lucida and stand.

I. At the level where all three arterial trunks are in open communication and posterior to the valves of the right systemico-carotid and left systemic trunks (slide 14, No. 5).

II. At the level where all three trunks are still in communication but the valves in right systemico-carotid and left systemic trunks are fully developed (slide 17, No. 1).

III. At level where main septum completely separates the pulmonary artery but the right systemico-carotid and left systemic are in communication (slide 19, No. 8).

IV. At level where all three trunks are completely separated; at front limit of valves and anterior to the cardiac cartilage (slide 22, No. 10).

A.Pu., arteria pulmonalis; *Car.C.*, cardiac cartilage; *L.S.A.*, left systemic arch; *R.S.C.*, right systemico-carotid.

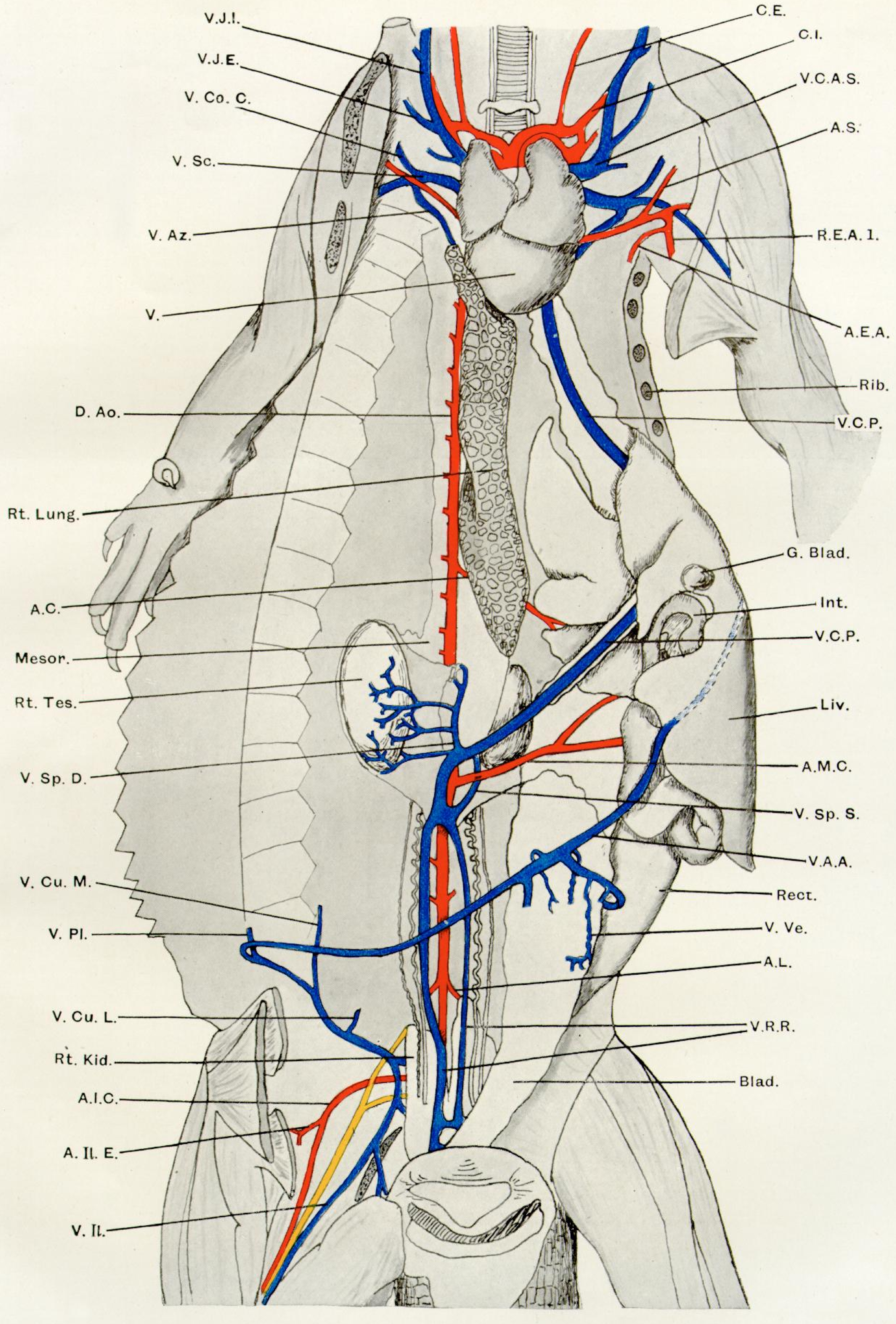


FIG. 1.

PLATE 6.

Fig. 1.—Diagrammatic sketch of a general view of the viscera of Sphenodon, with the alimentary canal displaced to the right.

Vessels.

A.C., arteria cœliaca; *A.E.A.*, arteria epigastrica anterior; *A.I.C.*, arteria iliaca communis; *A.Il.E.*, arteria iliaca externa; *A.L.*, arteria lumbalis; *A.M.C.*, arteria mesenterica communis; *A.S.*, arteria scapularis; *C.E.*, carotis externa; *C.I.*, carotis interna; *D.Ao.*, dorsal aorta; *R.E.A.* 1, ramus muscularis of arteria epigastrica; *V.*, ventricle; *V.A.A.*, vena abdominalis anterior; *V.Az.*, vena azygos; *V.C.A.S.*, vena cava anterior sinistra; *V.Co.C.*, vena coraco-clavicularis; *V.C.P.*, vena cava posterior; *V.Cu.L.*, vena cutanea lateralis; *V.Cu.M.*, Vena cutanea magna; *V.Il.*, vena iliaca communis; *V.J.E.*, vena jugularis externa; *V.J.I.*, vena jugularis interna; *V.Pl.*, vena parietalis lateralis; *V.R.R.*, venæ renales revehentes; *V.Sc.*, vena subclavia; *V.Sp.D.*, vena spermatica dextra; *V.Sp.S.*, vena spermatica sinistra; *V.Ve.*, venæ vesicæ.

Other Structures.

Blad., bladder; *G.Blad.*, gall bladder; *Int.*, intestine; *Liv.*, liver; *Mesor.*, mesorchium; *Rect.*, rectum; *Rib.*, cut end of ribs; *Rt.Kid.*, right kidney; *Rt.Lung*, right lung; *Rt.Tes.*, right testis.

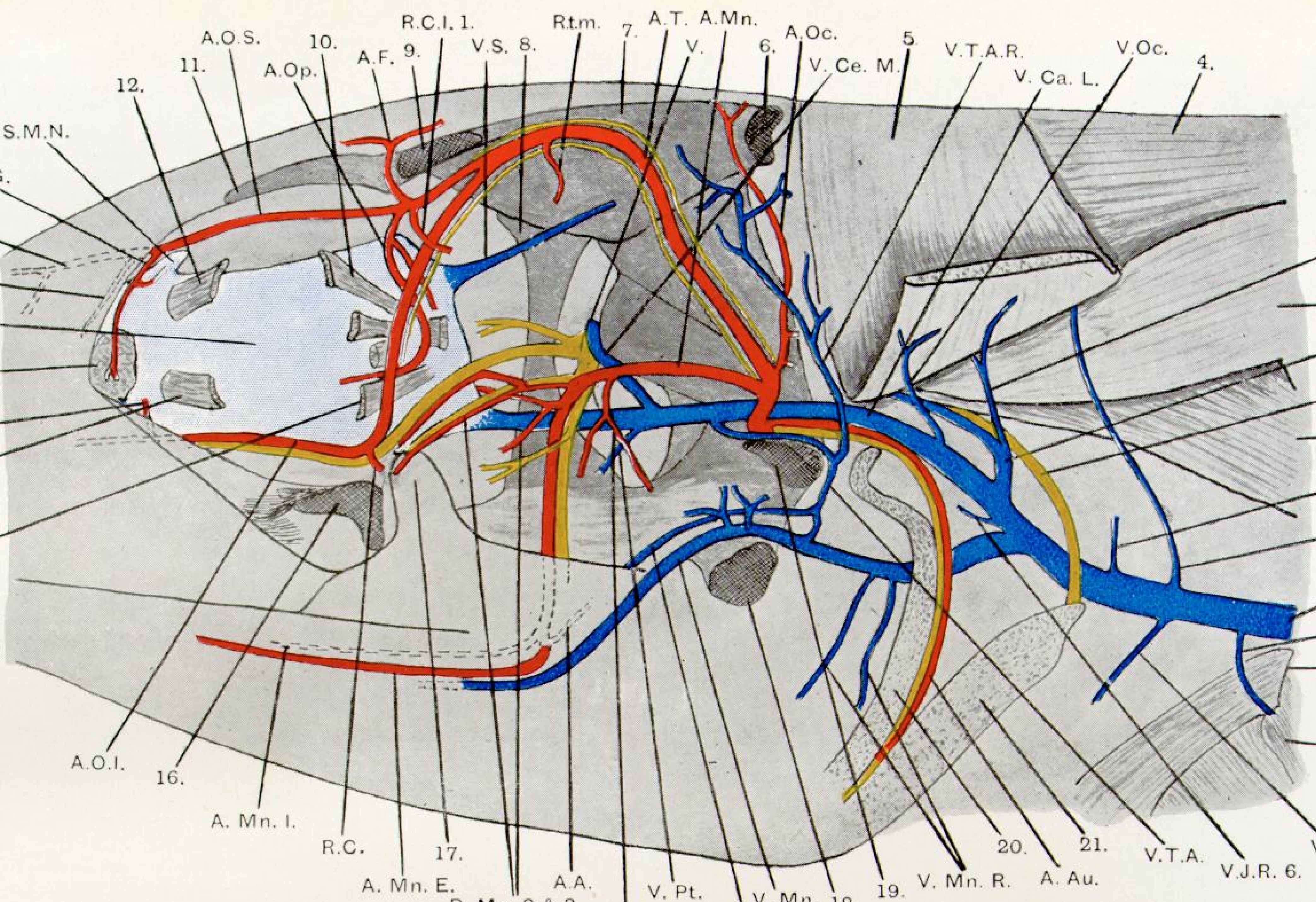


FIG. 2.

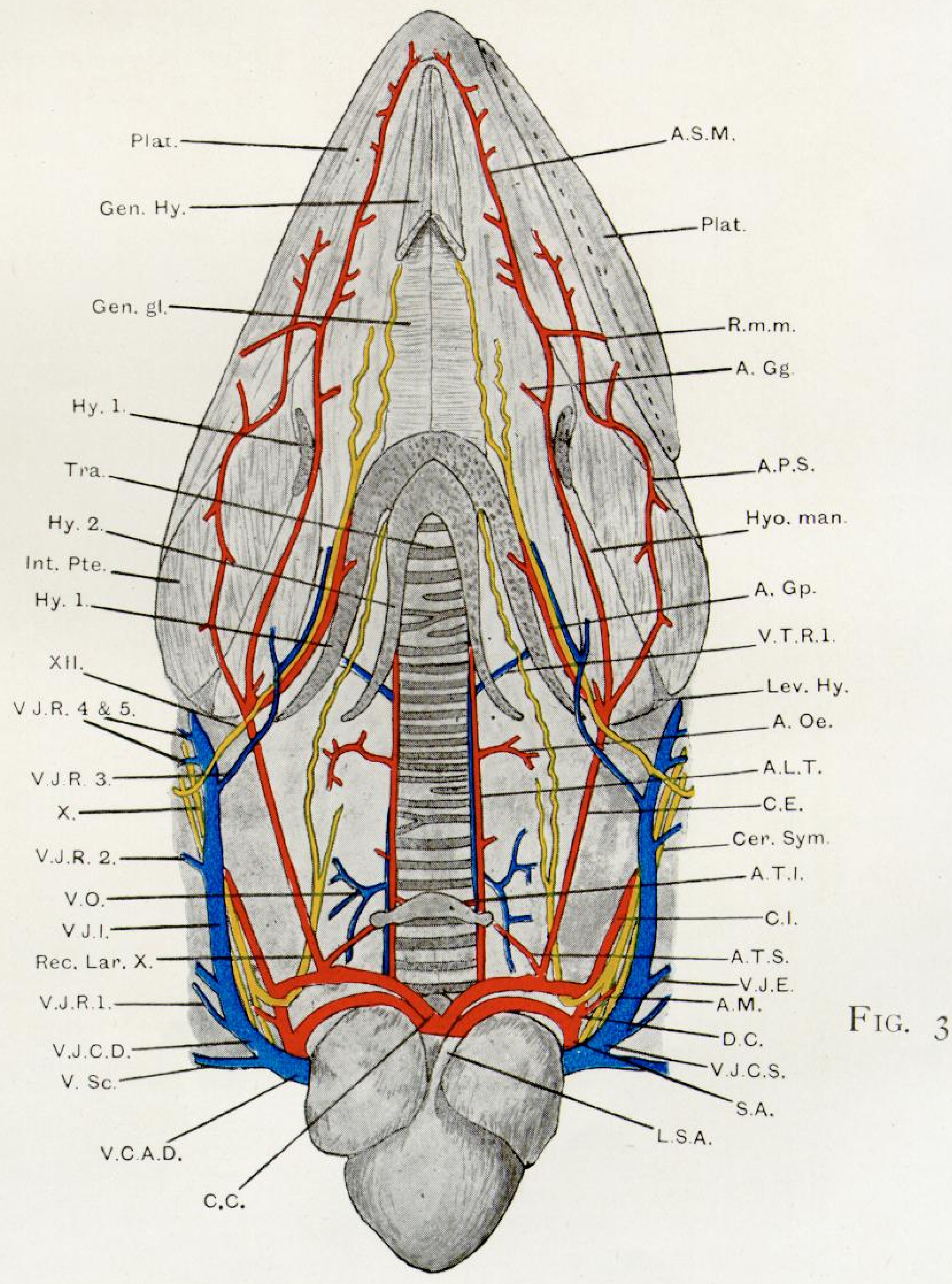


FIG. 3.

PLATE 7.

Fig. 2.—Diagrammatic sketch of the vessels shown in a lateral dissection of the head, certain of the bones having been removed.

Vessels.

A.A., arteria articularis; *A.Au.*, arteria auricularis; *A.F.*, arteria frontalis; *A.Mn.*, arteria mandibularis; *A.M.G.*, arteria musculo-glandaris; *A.Mn.E.*, arteria mandibularis externa; *A.Mn.I.*, arteria mandibularis interna; *A.N.*, arteria nasalis; *A.Oc.*, arteria occipitalis; *A.O.I.*, arteria orbitalis inferior; *A.Op.*, arteria ophthalmica; *A.O.S.*, arteria orbitalis superior; *A.T.*, arteria temporalis; *R.C.*, ramus coronoideus; *R.C.I.*, 1 and 2, rami musculares of arteria temporalis; *R.Mn.* 1, 2 and 3, rami musculares of arteria mandibularis; *R.m.n.*, ramus membranæ nictitantis; *R.t.m.*, ramus temporo-masseteris; *S.M.N.*, sinus membranæ nictitans; *S.O.*, sinus orbitalis; *V.Ca.L.*, vena capitis lateralis; *V.Ce.M.*, vena cerebralis media; *V.Ce.P.*, vena cerebralis posterior; *V.Ce.R.*, ramus muscularis of vena cerebralis posterior; *V.J.I.*, vena jugularis interna; *V.J.R.* 2–6, rami musculares of vena jugularis interna; *V.Mn.*, vena mandibularis; *V.Mn.I.*, vena mandibularis interna; *V.Mn.R.*, rami musculares of vena mandibularis; *V.Oc.*, vena occipitalis; *V.Pt.*, vena pterygoidea; *V.S.*, vena supra-temporalis; *V.T.A.*, vena tympanica anterior; *V.T.A.R.*, ramus muscularis of vena tympanica anterior.

Other Structures.

1, cleido-humeralis muscle; 2, ventral part of levator scapulæ; 3, dorsal part of levator scapulæ; 4, longissimus; 5, cucullaris; 6, cut end of parietal bone; 7, parietal bone; 8, columella cranii; 9, cut end of post-frontal bone; 10, rectus superior; 11, frontal bone; 12, obliquus superior; 13, Harderian gland; 14, obliquus inferior; 15, rectus inferior; 16, cut end of jugal bone; 17, coronoid process of mandible; 18, cut end of quadrato-jugal bone; 19, cut end of squamosal and quadrate bones; 20, anterior hyoid bone; 21, posterior hyoid bone; *V*, nervus trigeminus; *X*, vagus.

Fig. 3.—Diagrammatic sketch of the arteries and veins shown in a dissection of the head and neck from the ventral side.

Vessels.

A.Gg., arteria genio-glossa; *A.Gp.*, arteria glossopharyngeus; *A.L.T.*, arteria laryngeo-trachealis; *A.M.*, arteria muscularis cervicis; *A.Oe.*, arteria œsophagea; *A.P.S.*, arteria pterygoideus superficialis; *A.S.M.*, arteria submandibularis; *A.T.I.*, arteria thyreoidea inferior; *A.T.S.*, arteria thyreoidea superior; *C.C.*, carotis communis; *C.E.*, carotis externa; *C.I.*, carotis interna; *D.C.*, ductus caroticus; *L.S.A.*, left systemic arch; *R.m.m.*, ramus musculo-mandibularis; *S.A.*, systemic arch; *V.C.A.D.*, vena cava anterior dextra; *V.J.C.D.*, vena jugularis communis dextra; *V.J.C.S.*, vena jugularis communis sinistra; *V.J.E.*, vena jugularis externa; *V.J.I.*, vena jugularis interna; *V.J.R.* 1–5, rami musculares of vena jugulares; *V.O.*, venæ œsophageæ; *V.Sc.*, vena subclavia; *V.T.R.I.*, ramus muscularis of vena trachealis.

Other Structures.

Cer.Sym., cervical sympathetic; *Gen.gl.*, genio-glossus; *Gen.hy.*, genio-hyoid; *Hy.* 1, anterior cornu of hyoid; *Hy.* 2, posterior cornu of hyoid; *Hyo-man.*, hyo-mandibularis; *Int.Pte.*, internal pterygoid; *Lev.Hy.*, levator hyoidens; *Plat.*, platysma; *Rec.Lar.X.*, recurrent laryngeal of vagus; *Tra.*, trachea; X., vagus; XII., hypoglossal.

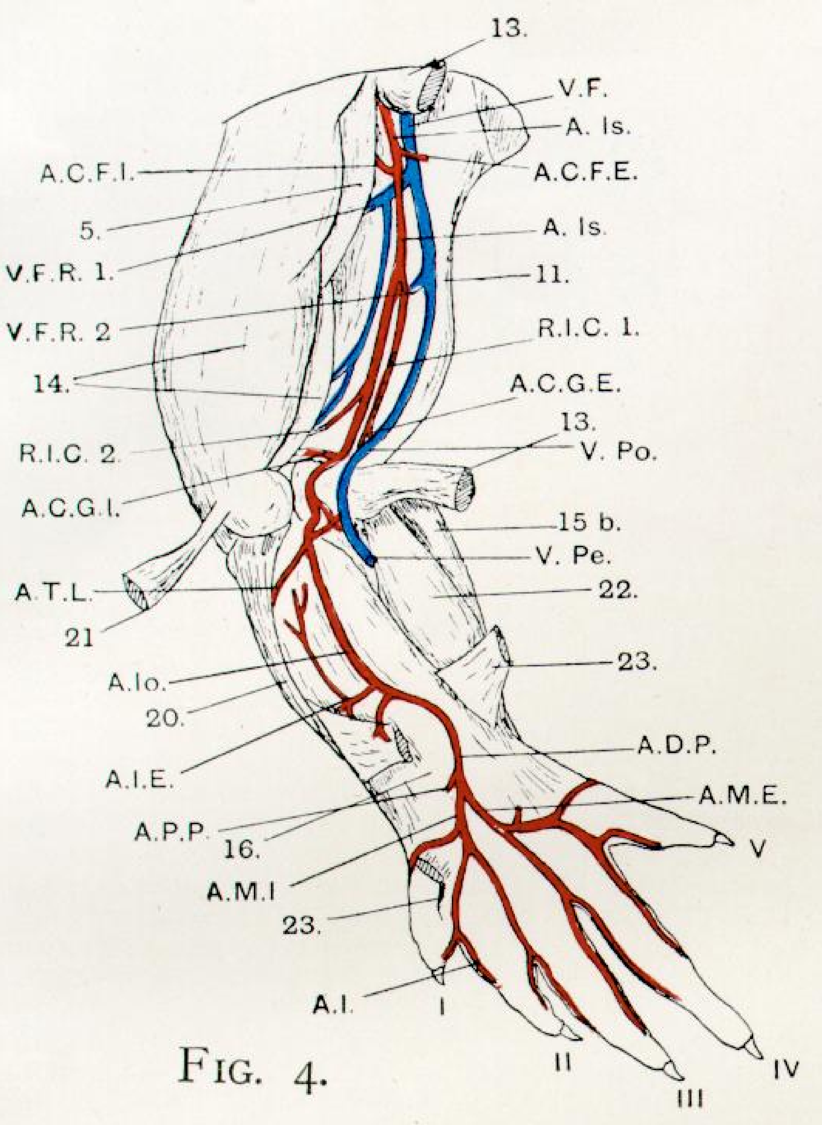


FIG. 4.

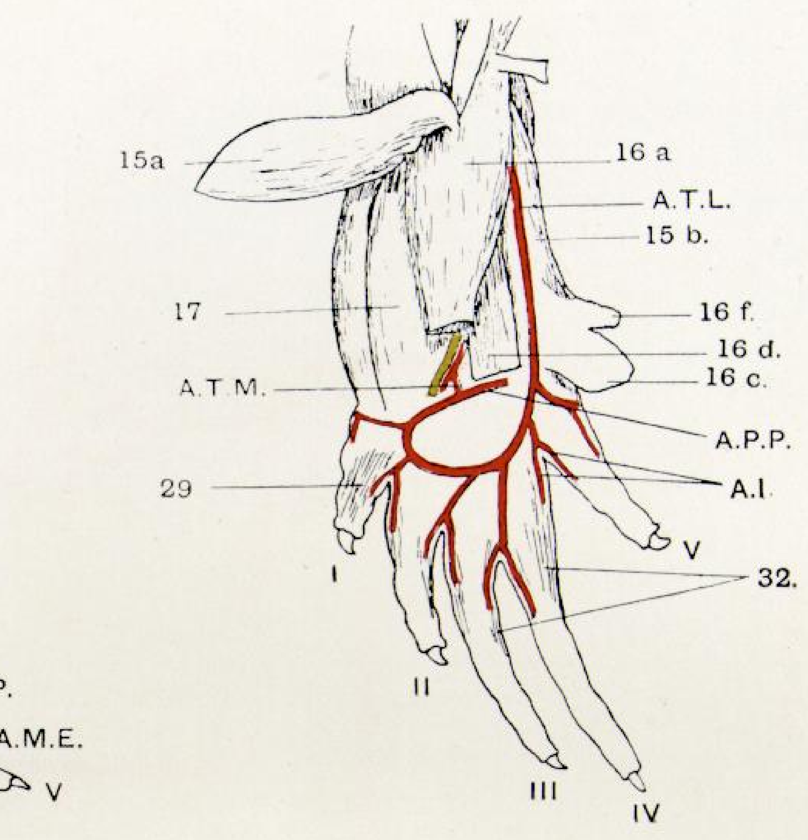


FIG. 5.

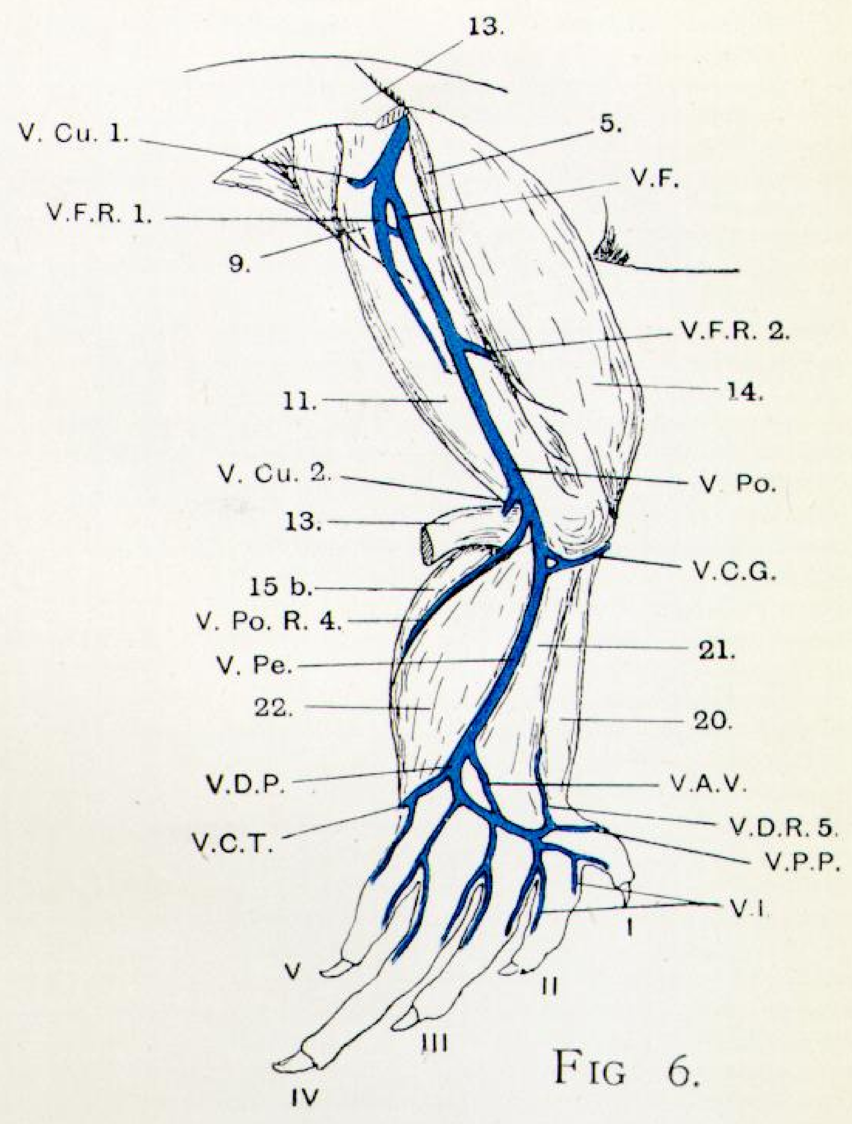


FIG 6.

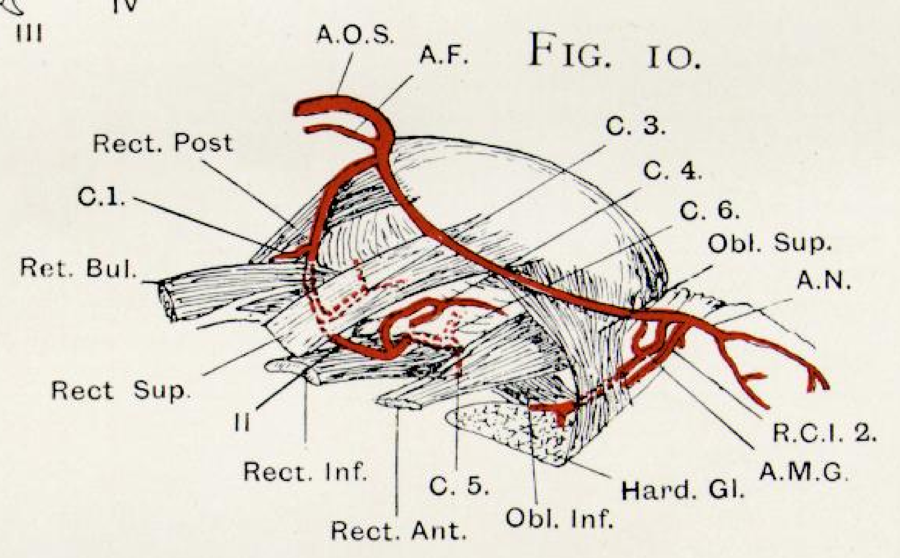


FIG. 10.

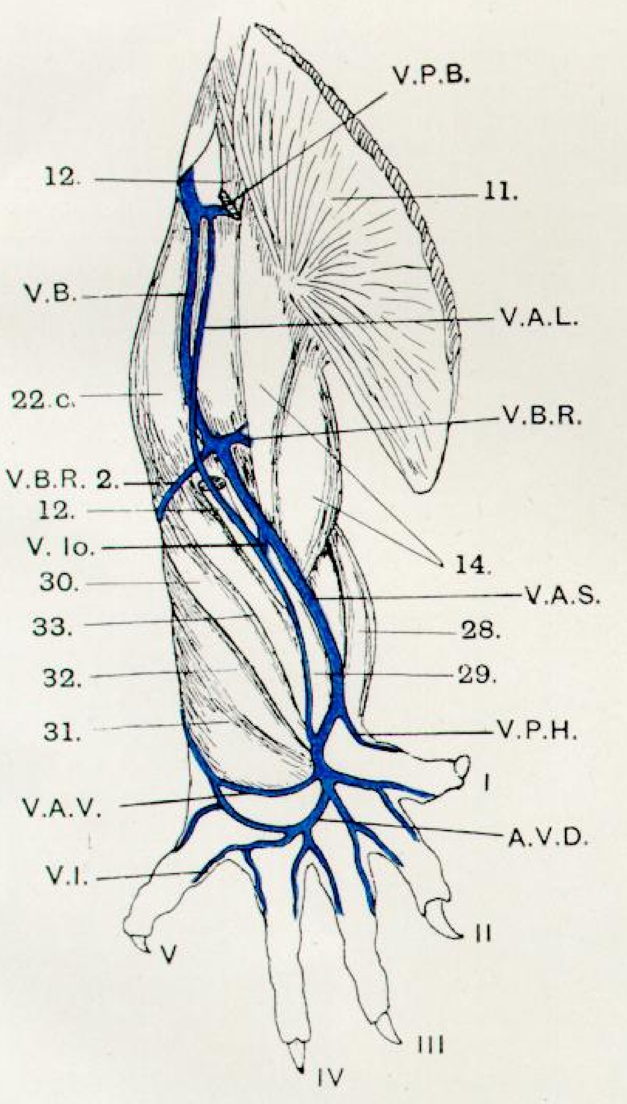


FIG. 7.

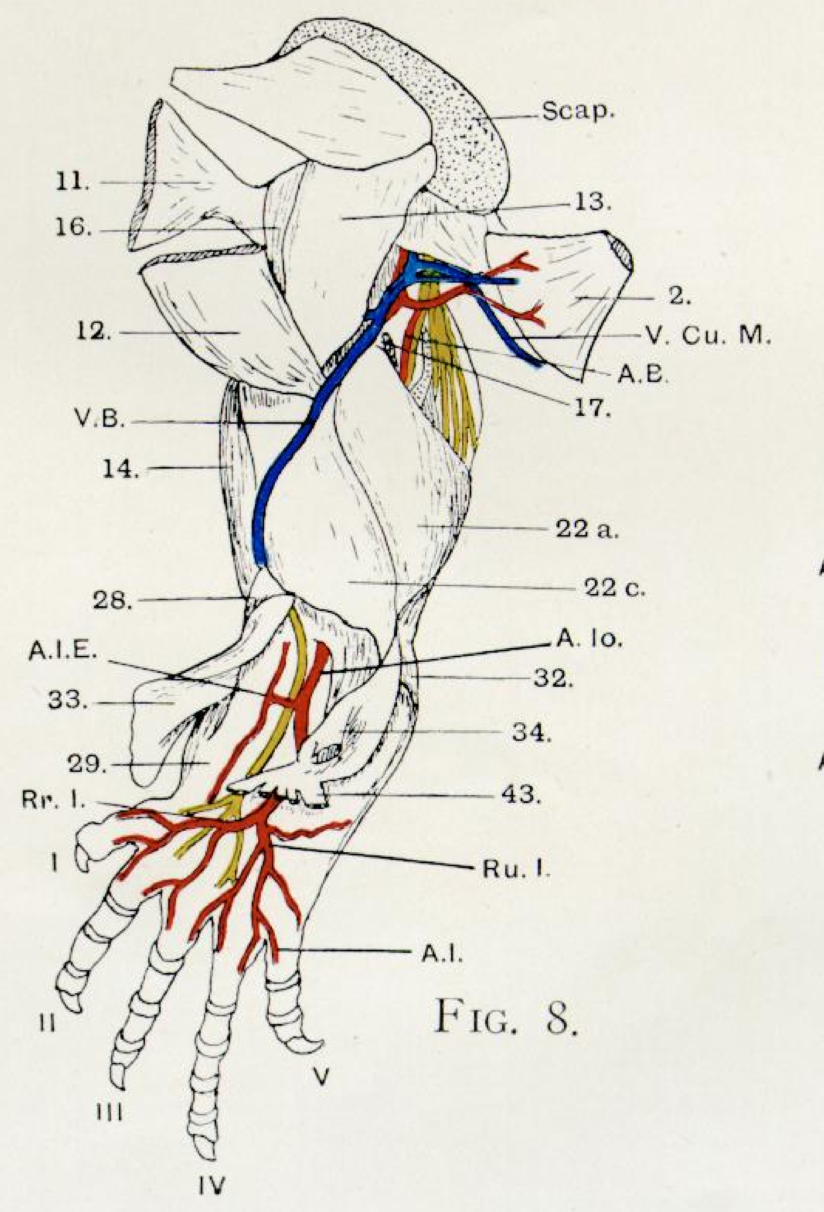


FIG. 8.

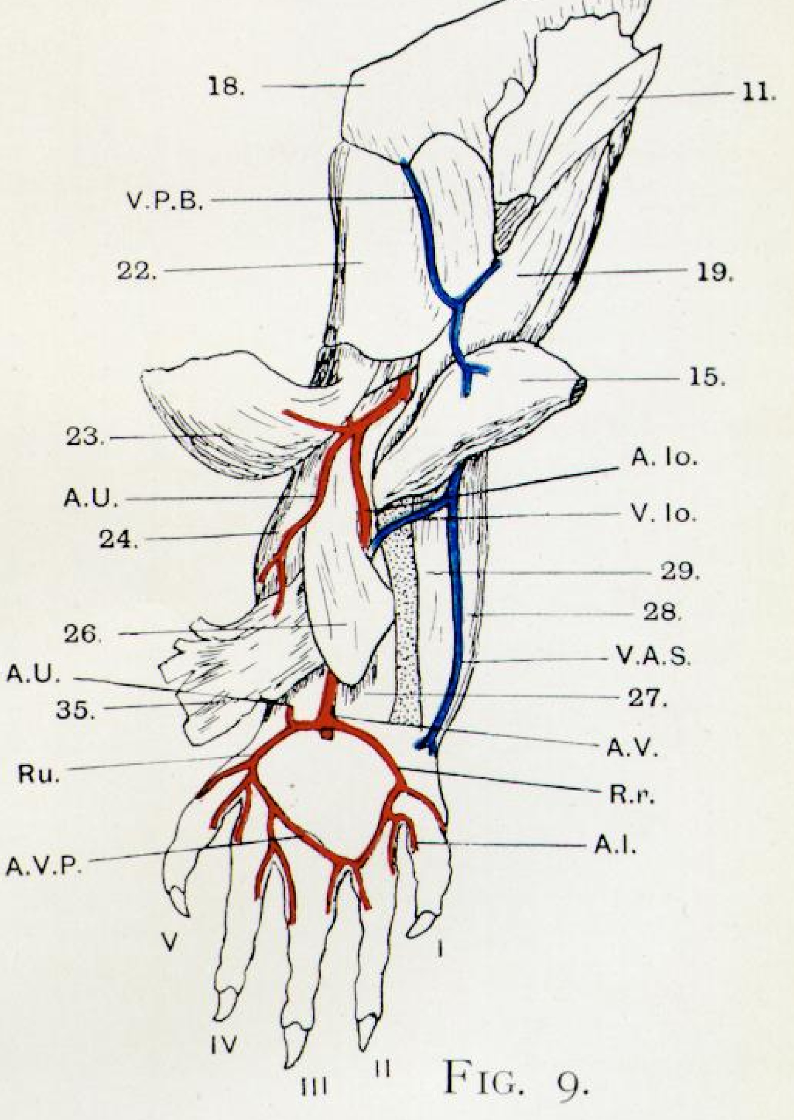


FIG. 9.

PLATE 8.

Figs. 4–10, Diagrammatic Sketches—

Fig. 4.—Vessels of the left hind limb viewed from the extensor surface.
Fig. 5.—Deeper arteries of the right hind foot viewed from the flexor (plantar) side.
Fig. 6.—Veins of the right hind limb viewed from the extensor surface.
Fig. 7.—Veins of the right fore limb viewed from the extensor surface.
Fig. 8.—Vessels of the left fore limb viewed from the extensor surface.
Fig. 9.—Vessels of the left fore limb viewed from the flexor surface.
Fig. 10.—Relation of the arteries to the muscles of the eye viewed from the inner aspect.

Muscles of Hind Limb.

5, ileo-femoralis; 9, ischio-trochantericus; 11, ischio-tibialis posticus; 13, ilio-fibularis; 14, extensor triceps; 15, gastrocnemius; 16, flexor digitorum communis profundus; 17 and 20, tibialis anticus; 21, extensor digitorum communis longus; 22, peroneus; 23, abductor et extensor hallucis longus; 29, abductor digitorum communis; 32, interossei planteres.

Arteries of Hind Limb.

A.C.F.E., arteria circumflexa femoris externa; *A.C.F.I.*, arteria circumflexa femoris interna; *A.C.G.E.*, arteria circumflexa genu externa; *A.C.G.I.*, arteria circumflexa genu interna; *A.D.P.*, arteria dorsalis pedis; *A.I.*, arteriæ interdigitales; *A.I.E.*, arteria interossea externa; *A.Io.*, arteria interossea; *A.Is.*, arteria ischiadica; *A.M.E.*, arteria metatarsalis externa; *A.M.I.*, arteria metatarsalis interna; *A.P.P.*, arteria perforans plantaris; *A.T.L.*, arteria tibialis lateralis; *A.T.M.*, arteria tibialis media; *R.I.C.* 1 and 2, rami musculares 1 and 2 of the arteria iliaca communis.

Veins of Hind Limb.

V.A.V., vena anastomotica arcus venosi; *V.C.G.*, vena circumflexa genu lateralis inferior; *V.C.T.*, vena circumflexa tarsi; *V.Cu.* 1 and 2, venæ cutaneæ; *V.D.P.*, vena dorsalis pedis; *V.D.R.* 5, ramus muscularis of the vena dorsalis pedis; *V.F.*, vena femoralis; *V.F.R.* 1 and 2, rami musculares of the vena femoralis; *V.I.*, venæ interdigitales; *V.Pe.*, vena peronea; *V.Po.*, vena poplitea; *V.Po.R.* 4, ramus muscularis of the vena poplitea; *V.P.P.*, vena præ-pollicis.

I Pollex; II–V digits (figs. 4–6).

Muscles of Fore Limb.

2, latissimus dorsi; 11, pectoralis; 12, cleido-humeralis; 13, dorsalis scapulæ; 14, supra-coracoideus; 15, coraco-brachialis; 17, scapulo-humeralis posterior; 18, scapulo-coraco-brachialis; 19, coraco-antibrachialis; 22, anconæus; 23, flexor-carpi-radialis; 24, flexor-digitorum-communis-profundus; 26, pronator teres; 27, pronator quadratus; 28, supinator; 29, extensor carpi radialis brevis; 30, extensor digitorum communis longus; 31, extensor carpi ulnaris; 32, anconæus quartus (richtiger quintus); 33, extensor carpi radialis longus; 34, abductor et extensor pollicis longus; 35, flexor digitorum communis sublimis; 43, extensor digitorum communis brevis.

Arteries of Fore Limb.

A.B., arteria bicipitalis; *A.I.*, arteriæ interdigitales; *A.I.E.*, arteria interossia externa; *A.Io.*, arteria interossea; *A.U.*, arteria ulnaris; *A.V.*, arteria volaris; *A.V.P.*, arcus volaris profundus; *R.r.*, ramus radialis; *Rr.* 1, ramus radialis of arcus dorsalis; *Ru.*, ramus ulnaris; *Ru.* 1, ramus ulnaris of arcus dorsalis.

Veins of Fore Limb.

A.V.D., arcus venosus dorsi manus; *V.A.L.*, vena anastomatica longa; *V.A.S.*, vena antibrachialis superficialis; *V.A.V.*, vena anastomatica arcus venosi; *V.B.*, vena branchialis; *V.B.R.*, *V.B.R.* 2, rami musculares of vena brachialis; *V.Cu.M.*, vena cutanea magna; *V.I.*, vena interdigitales; *V.Io.*, vena interossea; *V.P.B.*, vena profunda brachii; *V.P.H.*, vena præ-hallucis.

Sketch of Dissection of Eye from inner aspect (fig. 10).

Arteries.

A.F., arteria frontalis; *A.M.G.*, arteria musculo-glandaris; *A.N.*, arteria nasalis; *A.Op.*, arteria ophthalmica; *A.O.S.*, Arteria orbitalis superior; *C.* 1, branch to posterior rectus; *C.* 3, branch to superior rectus; *C.* 4, branch to back of eye; *C.* 5, branch to anterior rectus; *C.* 6, branch to inferior rectus.

Muscles.

Rect.Ant., rectus anterior; *Rect.Inf.*, rectus inferior; *Rect.Post.*, rectus posterior; *Rect.Sup.*, rectus superior; *Ret.Bul.*, retractor bulbi; *Obl.Inf.*, obliquus inferior; *Obl.Sup.*, obliquus superior; *Hard.Gl.*, Harderian gland; *II.*, optic nerve.