THE BLOOD VASCULAR SYSTEM OF AMBLYSTOMA TIGRINUM--(Green).

by

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SUMMARY.

A study has been made of the blood vascular system, exclusive of the heart, in Amblystoma tigrinum. As regards the arterial arches the fifth embryonic arch persists only in a few incompletely metamorphosed specimens, but vestigial ducti carotici and ducti Botalli occur in all specimens. A detailed account is given of the arterial system and of the venous system. Resemblances to Desmognathus are shown by the origin of the Vena Abdominalis from Venae Iliacae communes and by the presence of paired Arteriae Epigastricae . Resemblances to Spelerpes are shown in the opening of the Venae Subclaviae into ducti Cuvieri, and in the origin of each Arteria Cutanea magna (Bethge) from the Arteria Subclavia instead of from the Arteria Pulmonalis. In the non-persistence of postcardinal veins and of the fifth embryonic arch Amblystoma would appear to be less primitive than the majority of Urodela.

Contents.

1. INTRODUCTION.

It is commonplace knowledge in zoology that there is often less available information concerning a common laboratory type than there is with regard to relatively rarer forms. Amblystoma tigrinum is no exception in this respect.

On the whole the existing literature on the blood-vascular system of Urodele Amphibia is scanty. The heart however, has been fairly well described notably by Rabl (1887) Hopkins (1896), Bruner (1900) and Cords (1924). A description of the heart of Amblystoma can therefore be omitted here. This is all the more surprising when we consider the importance of the study of the Urodele blood system in revealing homologies with the lower and higher types.

As far back as 1888 Mauer discussed the gills and blood vessels of European Urodela. Bethge (1898) described the vascular system in general of the European lungless forms Triton and Spelerpes. In 1900 there appeared a fairly complete account of the blood system of Necturus maculatus by Santhoff and van Vorhis. Osawa's paper on the general anatomy of the Japanese salamander appeared in 1902 and was followed (1903) by Beddard's paper on the heart and vascular trunks of the same form. An outstanding landmark in the history of the subject was Seelye's (1906) description of the circulatory and respiratory systems of Desmognathus. This was the most complete account of the blood system in a Urodele up to that time. In her paper Miss Seelye made a comparison between the blood system of Desmognathus and that of Spelerpes as worked out by Bethge.

To my knowledge there has not yet been published any account of the blood-vascular system of Amblystoma. The present paper deals with the blood-vascular system of the adult Amblystoma tigrinum. The blood vascular system of the larval form has been reserved for a later paper.

2. MATERIAL AND METHODS.

The source of the material was the region immediately around Ninette, Manitoba. In this part of southern Manitoba these salamanders were for many years a yearly pest during the Fall when they would leave Pelican Lake and the other small lakes of this region in millions and climb up to the higher ground to dig themselves in for the Winter. Unfortunately, at the time when this investigation was begun, they had become exceedingly scarce so that it was only with difficulty that sufficient specimens were obtained for the completion of this paper. All the specimens were apparently adults showing no trace of external gills.

The specimens were assumed to be Amblystoma tigrinum since they agreed with Pratt's description of this species, being of a brownish color with the characteristic yellow markings, and possessing 2 plantar tubercles, 12 costal grooves and vomerine teeth in one patch. A few of the specimens were undoubtedly Amblystoma jeffersonianum possessing a single indistinct plantar tubercle, very long digits and the characteristic color and markings as described by Pratt (1923).

The work was done on these specimens. Some were injected with Prussian blue and some were dissected whilst fresh.

3. HEARD AND VASCULAR ROOTS

As in Amphibia generally the conus arteriosus springs from the anterior portion of the heart and merges almost immediately into the truncus arteriosus. The truncus arteriosus quickly breaks up into carotid, systemic and pulmonary arches (fig.1). The pulmonary trunks pass slightly outward and then loop back to supply the lungs. The right and left systemic trunks pass forwards and outwards so as to touch the muscles of the neck, and then unite in the mid line dorsal to and in front of the heart to form the dorsal aorta. Each carotid trunk passes forward to the base of the hyomandibular cartilage and there breaks up into external and internal carotid arteries. At this point lies the carotid gland. There is a functionless vessel (ductus caroticus) joining the carotid trunk to the systemic arch. There is also a similar vessel (ductus Botalli) joining the systemic and pulmonary arches. These are evidences of the more primitive larval condition though they are apparently functionless in the adult. As this was shown by Boas (1887) to be a typical Urodele phenomenon no further mention need be made of it here.

In an undetermined percentage of the specimens studied an extremely interesting condition was found to occur. Apparently an incomplete metamorphosis had taken place so that there remained on either side just back of the jaws a black gland-like mass which suggested the remains of a gill. This was supplied with blood by a branch from the systemic arch and also by a branch corresponding to the fifth embryonic arch. This arch was joined to both the systemic and pulmonary arches. Externally there was no sign of this gill except a slight depression in the skin.

In the same specimens there were present definite postcardinals which received branches from the lateral internal oblique muscles and joined to form a single vein just below the middle of the liver. The single vessel so formed entered the vena cava posterioris just prior to its entrance into the liver.

In the few specimens of Amblystoma jeffersonianum examined postcardinals were found to occur, but these also possessed the remains of a gill on either side similar to those described above in Amblystoma tigrinum. The occurrence was probably due to incomplete metamorphosis in both species.

4. CAROTID CIRCULATION.

Each common carotid artery passes cephalad and at the level of the base of the hyomandibular cartilage branches to form the external and internal carotid arteries. At the point where the common carotid branches but lying chiefly along the course of the internal carotid artery lies the carotid gland represented by an oval or roundish knot which because of an abundant supply of pigment cells has a black appearance. The carotid gland consists of a spongy reticular structure.

The internal carotid artery gives off a ramus muscularis which turns slightly backward and then follows the course of the upper jaw forwards supplying the temporal and masseter muscles. The internal carotid artery then turns upwards and forwards and divides into ophthalmic and cerebral branches. The point of division takes place just outside the cartilagineous wall of the orbit a little ventral to the foramen of the oculomotor nerve (fig.2).

From here the ophthalmic artery turns antero-laterally and pierces through the wall of the orbit. It passes over its ventral surface closely adhering to the sclerotic and pierces the sclerotic only on its anterior side.

The ophthalmic artery has the following branches:

(a) Ramus Muscularis- 1. A branch to the posterior rectus.

(b) Ramus muscularis- 2. A branch to the anterior part of the retractor bulbi.

(c) Ramus muscularis- 3. A branch to the superior rectus.

(d) Ramus hyaloideus- the last part of the ophthalmic itself.

The Cerebral branch separates from the ophthalmic branch and enters the cranium through the oculomotor foramen. Within the cranium it divides into an anterior and a posterior branch.

A. <u>The anterior branch</u> turns forward over the optic nerve and then runs along the outer ventral edge of the cerebral hemisphere and finally follows the olfactory tract inside the pia mater into the nasal capsule.

B. <u>The Posterior branch</u> of the cerebral carotid runs from its origin inwards and backwards along the upper lateral edge of the lobus infundibularis and then proceeds backwards. Behind the point of exit of the oculomotor nerve from the mid brain the arteries of both sides are connected dorsally from the hindmost part of the lobus infundibularis. Out of the single transversely lying vessel two new vessels emerge close to each other which run backwards and anastomose to form a single vessel the <u>arteria basilaris</u>. The basilar artery runs in the middle ventral fissure and backwards as the arteria spinalis ventralis on the ventral side of the nerve cord.

The following branches are given off from the hinder branch of the cerebral carotid:-

1. <u>Ramus mesencephali superior</u>- a branch which passes upwards and follows the course of the fissure between the optic lobe and the cerebellum.
2. <u>Ramus auditiva</u>- which arises from the arteria basilaris and with the anterior branch of the auditory nerve enters the auditory capsule.
3. <u>Ramus communicans cum Arteria vertebrali</u>- which comes off from the vertebral artery and joins the basilar artery in the region of the atlante occipital joint.

The external carotid passes forward from its point of origin and breaks up into three branches (fig.1): These originate together near the posterior end of the hyomandibular cartilage. They are:-

(a) Arteria thyroidea- a branch supplying the thyroid gland, the mylohyoid muscle, the hyomandibular cartilage, and giving off a branch at the level of the thyroid gland to supply the geniohyoid muscle and the tongue.

(b) Arteria mandibularis interna- the internal mandibular artery which supplies the mylohyoid, and the external and internal ceratohyoid muscles.

(c) Arteria mandibularis externa- the external mandibular artery, supplying the mylohyoid, submaxillary, and external ceratohyoid muscles, and extending forward to join by anastomosis with branch (b) at the anterior part of the head.

5. SYSTEMIC CIRCULATION.

The second pair of arches unite just posterior to the auditory organs to form the dorsal aorta. Each arch gives off three branches on each side, an arteria occipitalis, an arteria vertebralis collateralis, and an arteria maxillaris externa fig.1).

The arteria maxillaris externa leaves the systemic arch dorso-laterally, passes outwards, and forwards to divide, just posterior to the jaws into a branch to the lower and one to the upper jaw, the lower branch supplying the mylohyoid and submaxillary muscles, and the upper branch the temporal and masseter muscles, and the skin.

does not correspond to the arteria cutanea magna of the frog, or most other amphibia. Seelye calls the corresponding branch of the subclavian in Desmognathus the arteria sternalis and it certainly shows a closer correspondence to the arteria sternalis of mammals than it does with the arteria cutanea magna of amphibia. The term <u>arteria sternalis</u> when used in this paper may be taken to refer to this branch.

The rest of the subclavian artery where it enters the manus divides into two branches, the <u>arteria scapularis</u> supplying the shoulder girdle and the <u>arteria brachialis</u> which supplies the arm muscles with blood. The pectoralis and latissimus dorsi muscles receive blood from the arteria brachialis as do the supra coracoideus, the anconaeus, the deltoideus, the cleido-humeralis, the flexor carpi radialis, the flexor digitorum communis sublimis and the digits themselves. A branch of the arteria brachialis corresponding to the arteria interossea of Sphenodon supplies the extensor carpi radialis brevis and gives additional blood to the supra coracoideus (fig.3 and 4).

2. <u>Parietal arteries.</u>

The aorta gives off nine paired parietal arteries between the front and hind limbs although one member of a pair is frequently absent. The parietal arteries all join the vertebral arteries.

3. <u>Arteriae genitales.</u>

The genital arteries-two paired arteries supply the ovaries or testes.

4. The coeliaco mesenteric axis or arteria intestinalis communis- This arises from the dorsal aorta and gives off numerous branches.

(a) Antero gastric- This artery supplies the cardiac portion of the stomach.

(b) Arteria hepatica- This is the main artery supplying the liver.

(c) Arteria gastrico-duodenalis- This is a branch to the pyloric end of the stomach, the duodenum and pancreas.

(d) Arteria lienalis- This artery supplies blood to the spleen.

(e) Arteriae mesentericae- These two branches supply blood to the mesentery and intestine.

(f) Arteria haemorrhoidalis- This branch provides blood for the rectum.

5. Arteria mesenterica posterior- This branch arises from the dorsal aorta two segments posterior to the point of origin of the coeliaco mesenteric axis and supplies the posterior end of the intestine and mesentery.

6. Arteriae renales- These are paired renal branches to the kidneys.

7. Arteriae epigastricae- These are paired vessels arising from the dorsal aorta just anterior to the iliac arteries. These are comparatively large arteries which run along the ventro lateral body wall giving off branches to

supply the muscles and joining by anastomosis with the arteriae sternales on either side, so as to form a continuous vessel. This may be a primitive forerunner of the condition in mammals- a series of segmentally arranged vertebral arteries which were once all connected by anastomoses: later the connections with the aorta of the middle part of the series became lost and the anastomoses made one continuous lateral artery along each ventro lateral wall of the trunk, the arteria sternalis of mammals.

8. Arteriae iliacae- The iliac artery, on either side, leaves the dorsal aorta near the posterior end of the kidney, passes laterally across the dorsal surface of the kidney and then dips sharply backwards at an angle of about 30 degrees as it enters the leg. Immediately on its entrance into the leg it swells and from the enlargement so formed arise several branches:-

1. A branch to the ischio caudalis muscle.
2. A branch to the upper portion of the extensor triceps muscle.
3. A branch to the upper portion of the semimembranosus muscle.
4. The arteria ischiadica. (fig.5 and 6)

The arteria ischiadica continues distally and gives off branches to the femoro-fibularis and glutaeus maximus muscles, a branch to the gracilis and a branch to the lower part of the semimembranosus, and continues distally to supply the flexor digitorum profundus. It gives off just above the level of the knee a branch the arteria interossea from which arise two branches, one passing outward as the arteria cutanea while the inner branch, the arteria tibialis lateralis passes under the knee to the extensor surface of the hind limb. The arteria tibialis lateralis supplies the extensor digitorum communis longus muscle and the digits themselves by means of the arteriae interdigitales.

9. Arteria caudalis- The caudal artery runs backward from the end of the dorsal aorta and supplies the blood to the tail.

6. PULMONARY CIRCULATION.

Each arteria pulmonalis is well developed though smaller than either of the other arches. It sends off an arteria pharyngea to the ventral wall of the pharynx. There is no branch corresponding to the arteria cutanea magna of the frog. This would seem to indicate a more complete aeration of the blood in the lungs or that these more sluggish forms find the aeration which takes place in the capillary endings of various vessels in the skin sufficient for their needs.

7. ANTERIOR VENOUS SYSTEM.

The blood from the anterior region of the body is brought to the sinus venosus through each ductus Cuvieri by a large vein the vena jugularis externa and a smaller vein the vena jugularis interna (fig.7).

The vena jugularis externa is formed by the union of the vena maxillaris inferioris and several small branches which receive blood from the mylohyoid, geniohyoid, and internal ceratohyoid muscles, the hyomandibular plate, and the thyroid gland. The vena maxillaris inferioris arises at the tip of the jaw from an anastomosis with the vein of the opposite side and follows the course of the lower jaw most of the way back receiving blood from the mylohyoid and submaxillary muscles. It then passes in almost to the centre line and joins with the branches from the tongue, hyomandibular plate and floor of the mouth to form the external jugular. On its backward course the vena jugularis externa receives a short branch from the thyroid gland.

The vena jugularis interna is formed by the union of the vena maxillaris superioris, a branch from the central nervous system, and branches from the temporal and masseter muscles. The vena maxillaris superioris is made up of branches from each side of the eyeball.

The blood from the forebrain is removed by two vessels, the lateral prosencephalic veins, which begin at the anterior dorsal part of the forebrain, pass posteriorly along its dorso-lateral edge to unite at the anterior dorsal edge of the mid brain into a transverse vessel the posterior diencephalic vein. The blood from the nerve cord is removed from the hindermost part of the cord by the terminal vein which runs anteriorly along the mid dorsal edge of the nerve cord within the vertebral column, becoming at about the level of the anterior edge of the kidneys the internal dorsal vertebral vein. The internal dorsal vertebral vein receives small branches the intervertebral veins from the vertebrae. At the junction of the nerve cord and hind brain the internal dorsal vertebral vein breaks into two branches the cranial occipital veins. The cranial occipital veins then pass forward along the dorsal lateral edge of the brain to join with the posterior diencephalic vein and the common vessel so formed passed through the trigeminal foramen and enters the internal jugular vein.

Opening into the ductus Cuvieri at the same point as the vena jugularis externa is the large musculo-cutaneous vein (vena cutanea magna). This receives in its course numerous branches from the sides of the animal(from the muscles and skin), and one relatively large branch from the skin of the dorso-lateral part of the head that seems to correspond to Seelye's (and Bethge's) "vena cutanea parva" (fig.7).

The blood from the manus is removed by the vena brachialis. The digits, the extensor digitorum, anconaeus quartus, extensor carpi radialis brevis, the supra coracoideus, the cleido humeralis, and anconaeus muscles all supply blood to the vena brachialis, as does also the pectoralis. The vena brachialis joins with the vena cutanea magna and the vena coraco-clavicularis (bringing blood from the latissimus dorsi muscle and from the skin) to form the subclavian vein before entering the Cuvierian duct.

The venae pulmonales bringing blood from the lungs unite and empty into the base of the sinus venosus by a common pulmonary vein from the right dorsal side.

8. POSTERIOR VENOUS SYSTEM.

Most of the blood from the liver is returned through the vena hepatica revehens which arises from many capillary branches within the substance of the liver and emerges as a large vessel at the ventral anterior end of the liver to enter the sinus venosus (fig.8 and 9).

The remainder of the blodd from the posterior region of the body is brought to the sinus venosus by the vena cava posterioris, vena porta hepatica and vena abdominalis.

The vena cava posterioris arises by branches, the venae renales revehentes, from the kidneys, passes forward receiving branches from the rectum, the intestine and mesentery (venae mesentericae), the genital organs, the pancreas, and a branch from the spleen, traverses the right dorsal portion of the liver and opens with the vena hepatica revehens from the ventral side of the liver into the sinus venosus (fig.9).

As was mentioned before, some of the specimens examined were thought to be incompletely metamorphosed on account of their possession of the remains of a gill on either side. These specimens possessed definite postcardinal vessels, the right and left members of which joined to form a single vessel which entered the vena cava posterioris just before its entrance into the liver. Most of the specimens, however, showed no traces of either gills nor postcardinals. These latter were assumed to be (completely metamorphosed) adults. The absence of postcardinals in the adult Amblystoma tigrinum would seem to be an indication of a less primitive condition than that found in certain salamanders such as Salamandra maculosa.

The vena abdominalis is formed not by branches from the venae iliacae on each side but by two branches, rami abdominales, from the venae iliacae communes as they pass along the latero dorsal sides of the kidneys, and by a branch from the bladder (vena vesicularis) and branches from the ventral body wall (venae musculares). In addition it receives several branches from the mesentery (venae mesentericae) and a branch from the rectum (vena haemorrhoidalis).

The rami abdominales receive blood from the tail (vena caudalis), a short branch from the hinder end of the bladder and the branches from the hind legs (venae iliacae). Each ramus abdominalis also receives a branch from the ventral body wall and a branch from the dorso-lateral portion of the skin just back of the hind leg. The two rami abdominales join to form the vena abdominalis which enters the vena porta hepatica. The rami abdominales give off numerous branches to the kidneys so that some of the blood they receive passes through the capillaries of the liver while part passes through the kidneys entering them through the venae renales advehentes (fig.8).

The vena porta hepatica receives branches from the mesentery (venae mesenterica), the stomach (venae gastricae), the stomach and duodenum (vena gastrico-duodenalis), and the oesophagus (vena oesophagea), It also receives the vena abdominalis so that it appears almost as a branch of the hepatic portal vein (fig.8 and 9).

In the hind leg the digits are drained by the venae interdigitales which join to form the vena peronea. The vena peronea receives a branch at the knee from the extensor digitorum communis longus muscle. Just above this point it enters the vena poplitea which receives two branches from the skin (venae cutaneae), and branches from the gastrocnemius, ilio fibularis, and pubo-tibialis muscles. The vena poplitea enters the vena femoralis which receives branches from the gracilis, femoro-fibularis, extensor triceps, semimembranosus and glutaeus maximus muscles. The vena femoralis as it leaves the leg enters the iliac vein which joins the remus abdominalis near the posterior end of the kidney.

The vena caudalis drains the musculature of the tail and enters both the rami abdominales at one point in the mid line just posterior to the kidneys.

GENERAL CONCLUSIONS.

As compared with the two Urodele types whose blood-vascular system is fairly well known, namely Desmognathus and Spelerpes, Amblystoma tigrinum agrees with the former type in having a Vena Abdominalis originating from Venae Iliacae communes and in having paired Arteriae Epigastricae arising from the aorta in front of the Arteriae Iliacae. On the other hand Amblystoma resembles Spelerpes in that the Venae Subclaviae open into the ducti Cuvieri and not as in Desmognathus directly into the sinus venosus. A further resemblance to Spelerpes occurs in the origin of each Arteria Cutanea magna from the Arteria Subclavia instead of from the Arteria Pulmonalis.

In its lack of postcardinal veins, and in the non-persistence of the fifth embryonic arterial arch, Amblystoma would appear to be less primitive than the majority of Urodela.

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LIST OF FIGURES.

LIST OF ABBREVIATIONS.

Vessels.

A.C.M.	Arteria Coeliaco-mesenterica.
A.C.M. ant-gast.	Arteria antero-gastrica.
A.C.M. gast-duo.	Arteria gastrico-duodenalis.
A.C.M. haem.	Arteria haemorrhoidalis.
A.C.M. hep.	Arteria hepatica.
A.C.M. lien.	Arteria lienalis.
A.C.M. mes.	Arteria mesenterica.
A.E.	Arteria epigastrica.
A.G.	Arteria genitales.
A.I.	Arteriae interdigitales.
A.Il.	Arteria iliaca.
A.Io.	Arteria interossea.
A.Io. cut.	Arteria cutanea.
A.Io. tib.	Arteria tibialis lateralis.
A.Is.	Arteria ischiadica.
A.M.E.	Arteria maxillaris externa.
A.M.P.	Arteria mesenterica posterioris.
A.Oc.	Arteria occipitalis.
A.P.	Arteriae parietales.
A.R.	Arteriae renales.
A.S.C.	Arteria subclavia.
A.S.C.ab.	Arteria brachialis.
A.S.C.as.	Arteria sternalis.

A.S.C.sc.	Arteria scapularis.
A.V.	Arteria vertebralis.
C.E.	Carotis externa.
C.E.me.	Arteria mandibularis externa.
C.E.mi.	Arteria mandibularis interna.
C.E.th.	Arteria thyroidea.
D.Ao.	Dorsal Aorta.
V.A.	Vena abdominalis.
V.A.haem.	Vena haemorrhoidalis.
V.A.vm.	Vena muscularis.
V.A. v.mes.	Vena vesicularis.
V.B.	Vena brachialis.
V.C.	Vena caudalis.
V.C.C.	Vena coraco-clavicularis.
V.C.M.	Vena cutanea magna.
V.C.P.	Vena cava posterioris.
V.F.	Vena femoralis.
V.H.R.	Vena hepatica revehens.
V.I.	Venae interdigitales.
V.Il.C.	Vena iliaca communis.
V.J.E.	Vena jugularis externa.
V.J.E.max.inf.	Vena maxillaris inferioris.
V.J.E.ling.	Vena lingualis.
V.J.I.	Vena jugularis interna.
V.J.I.sup.	Vena maxillaris superioris.
V.P.	Vena pulmonalis.

V.Pe.	Vena peronea.
V.P.H.	Vena porta hepatica.
V.P.H.gast.	Venae gastricae.
V.P.H.gast-duo.	Vena gastrico-duodenalis.
C.P.H.mes.	Venae mesentericae.
V.P.H.oes.	Vena oesophagea.
V.Po.	Vena poplitea.
V.R.R.	Venae renales revehentes.

Muscles.

1. Anconaeus.
2. Anconaeus quartus.
3. Cleido-humeralis.
4. Extensor carpi radialis brevis.
5. Extensor digitorum communis longus.
6. Extensor triceps.
7. Femoro-fibularis.
8. Flexor carpi radialis.
9. Flexor communis brevis.
10. Flexor digitorum communis longus.
11. Flexor digitorum communis profundus.
12. Flexor digitorum communis sublimis.
13. Gastrocnemius.
14. Geniohyoideus.
15. Glutaeus maximus.

16.	Gracilis.
17.	Latissimus dorsi.
18.	Pectoralis.
19.	Semimembranosus.
20.	Supra-coracoideus.
21.	Tibialis anticus.

Other Structures.

I	Auditory Capsule.
II	Carotid Gland.
III	Cerebral Hemisphere.
IV	Hyomandibular Cartilage.
V	Nasal Capsule.
VI	Thyroid Gland.

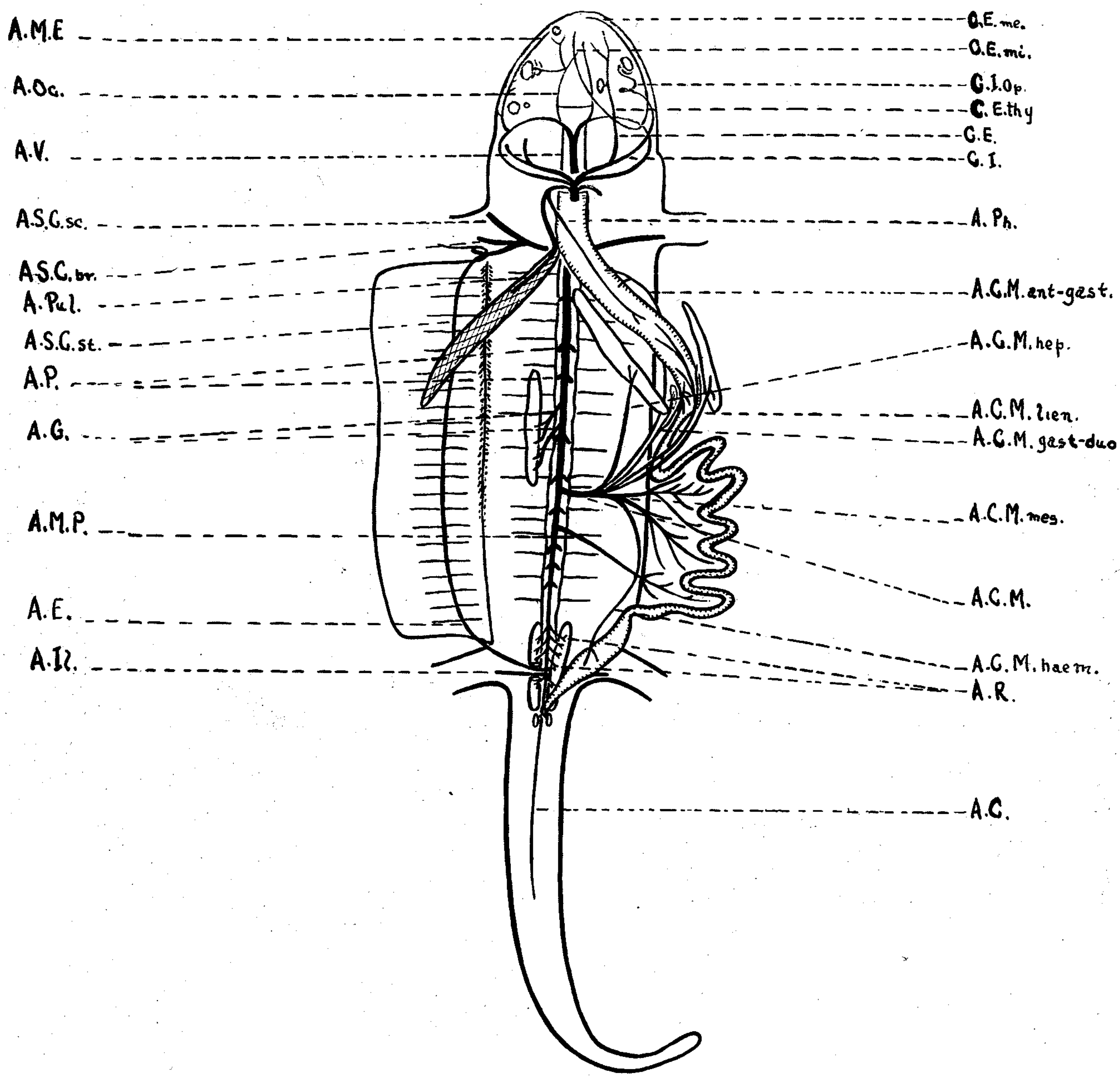

Fig. 1. General View of the Arterial System.(X.$\frac{2}{3}$)

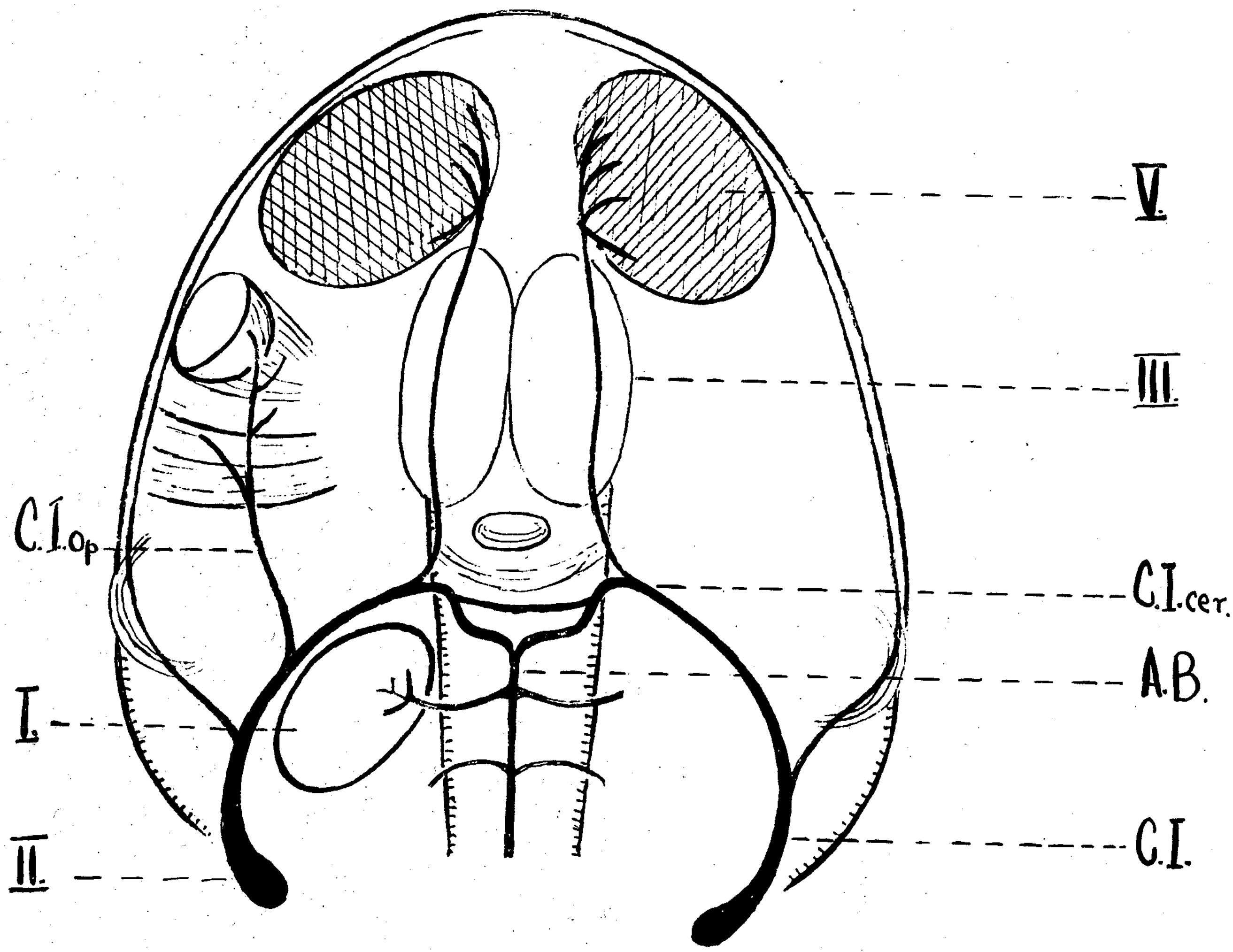

Fig. 2. Internal Carotid Arteries, showing Cerebral Branches.(X.3)

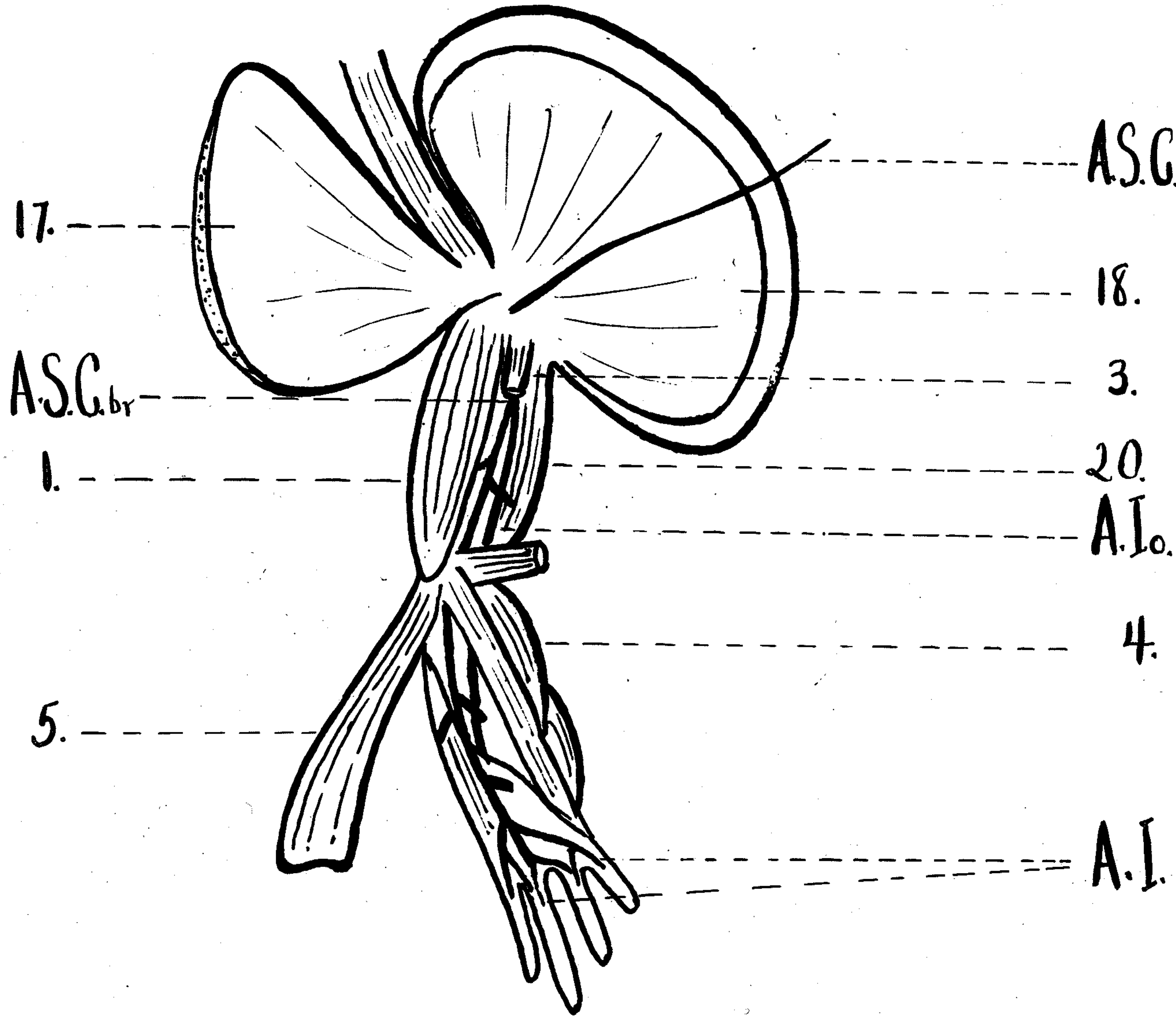

Fig. 3. Arteries of the Right Manus from the Extensor Side. (X.4)

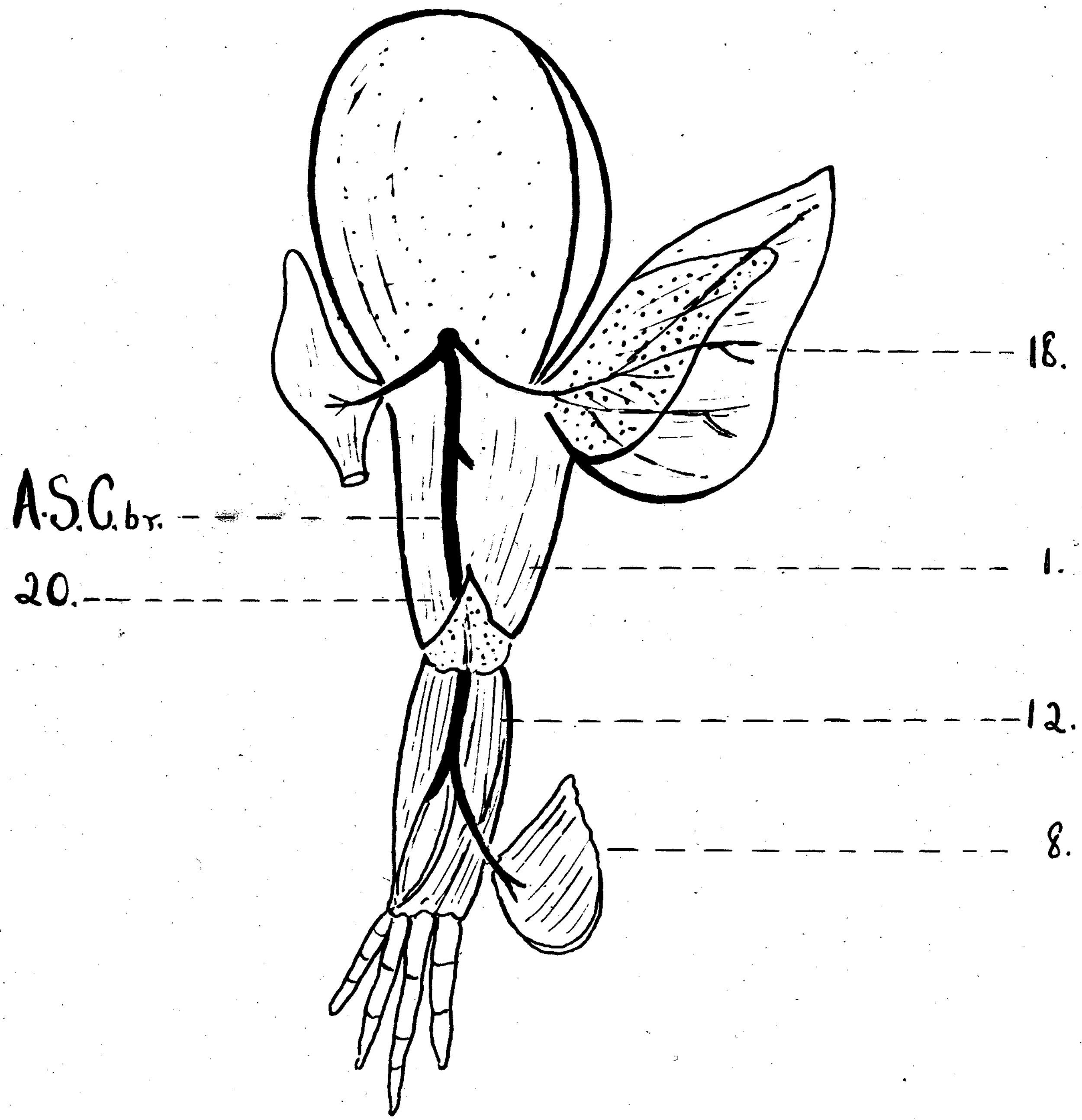

Fig. 4. Arteries of the Right Manus from the Flexor Side. (X.4)

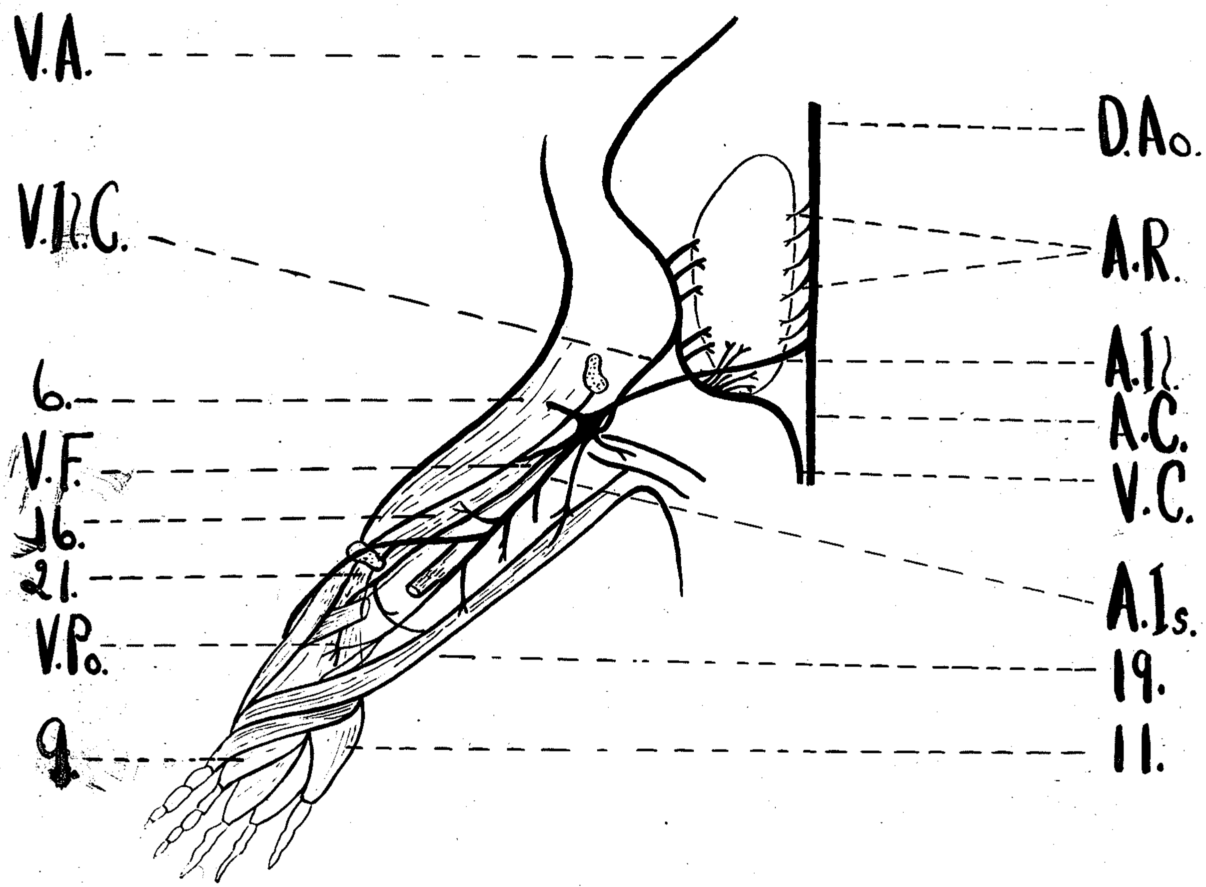

Fig. 5. Arteries and Veins of the Left Pes from the Flexor Side.(X.3)

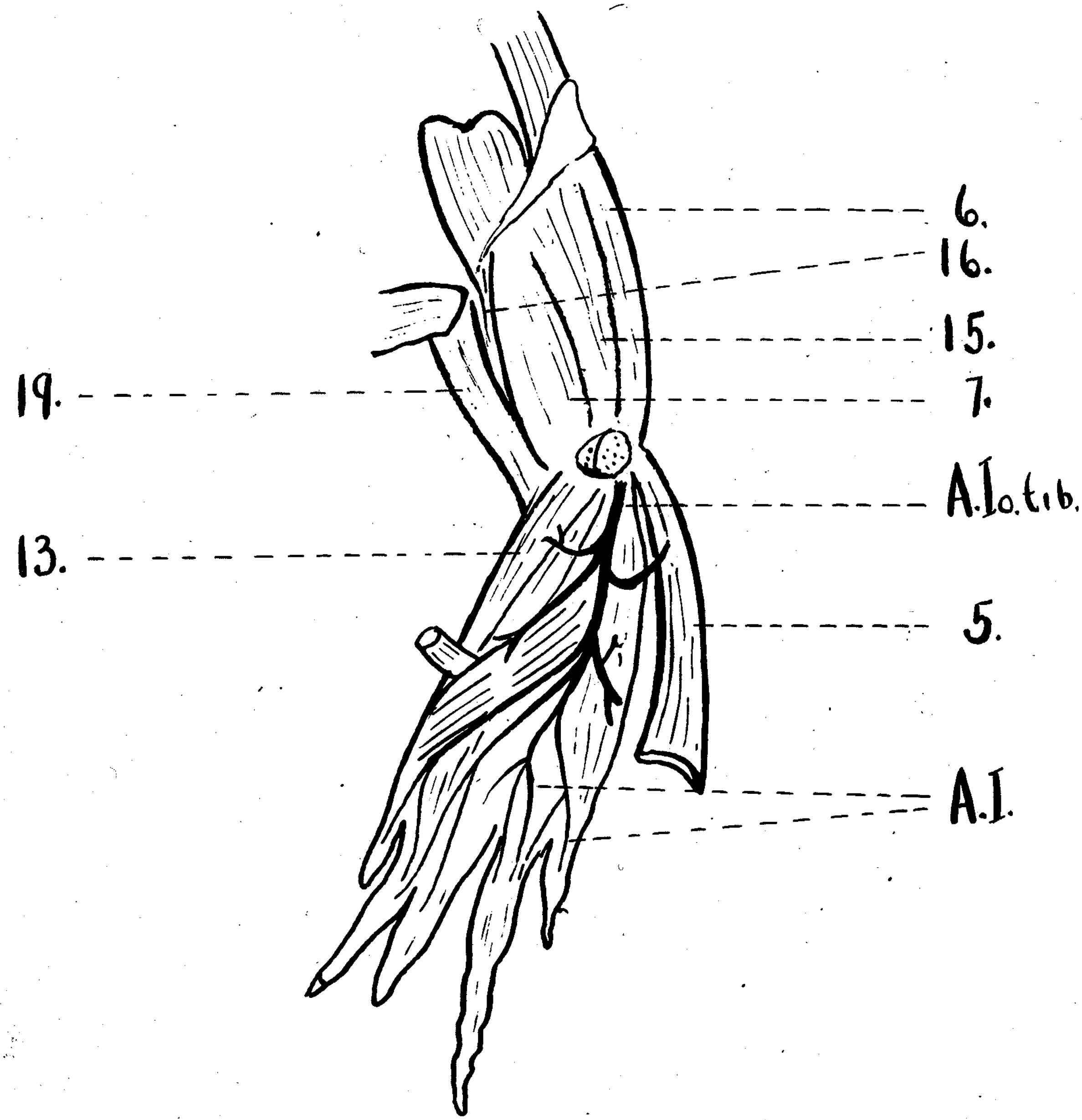

Fig. 6. Arteries of the Left Pes from the Extensor Side. (X.3)

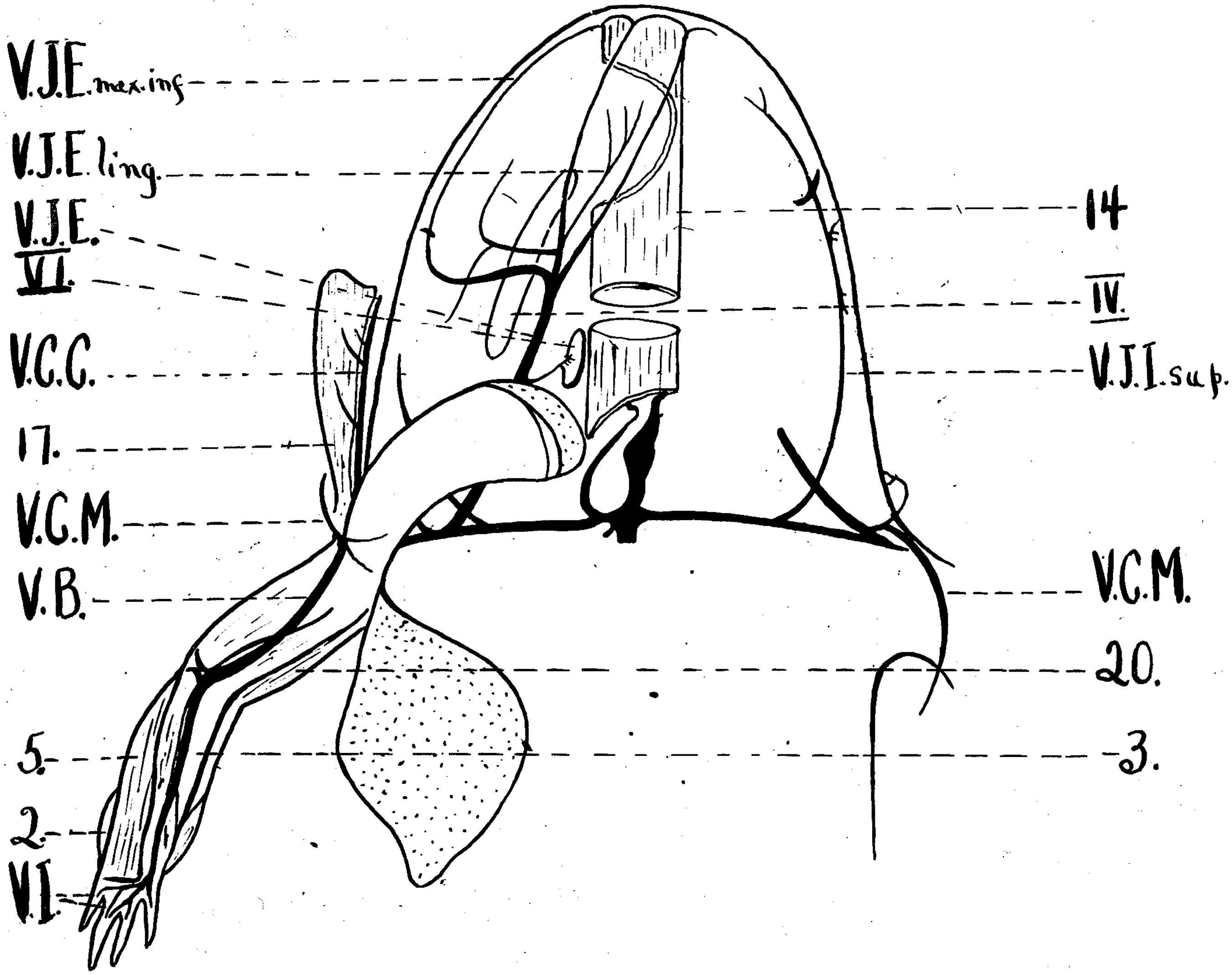

Fig. 7. The Veins of the Head and Right Manus. (X.2)

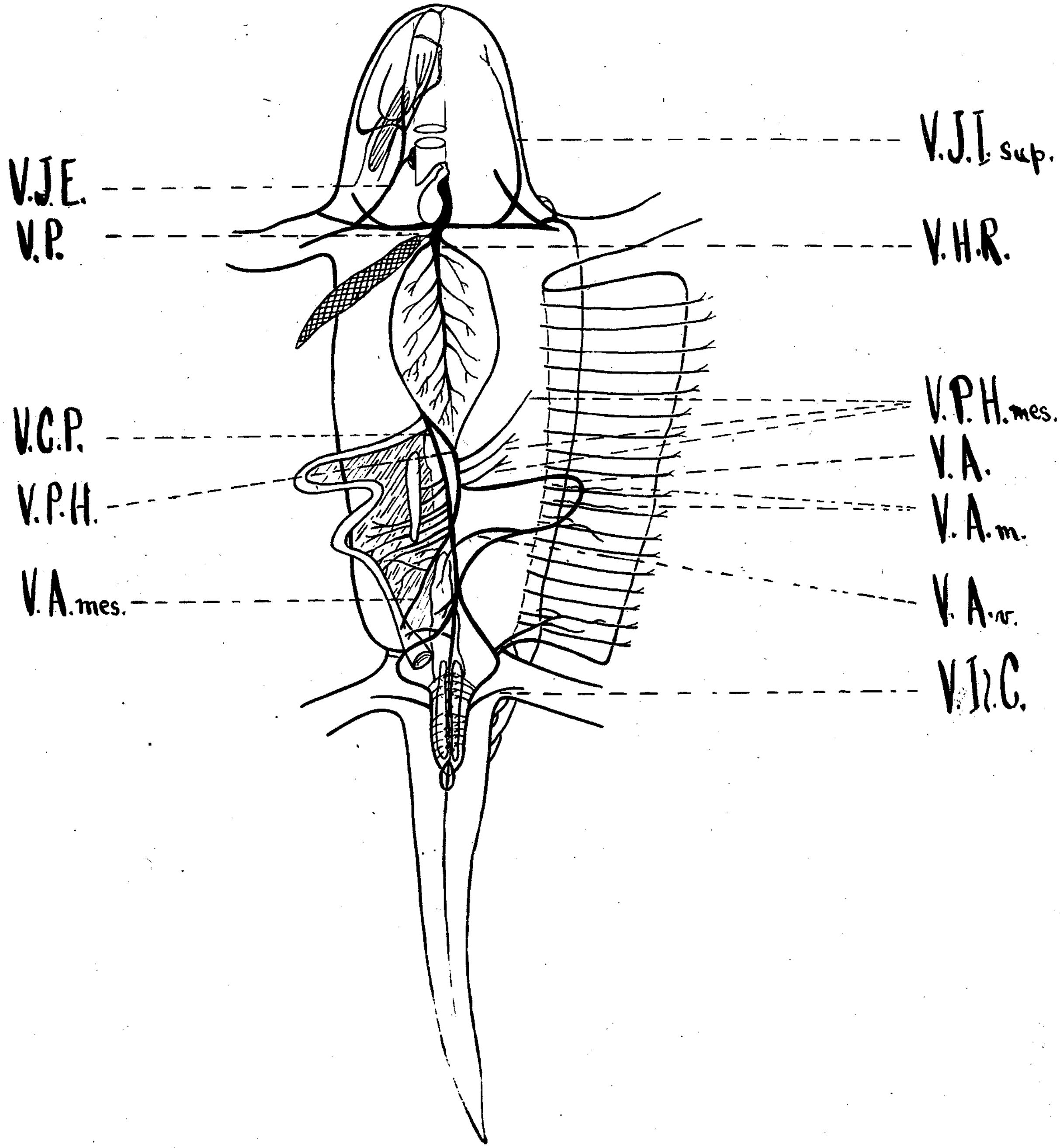

Fig. 8. General View of the Venous System.(X.$\frac{2}{3}$)

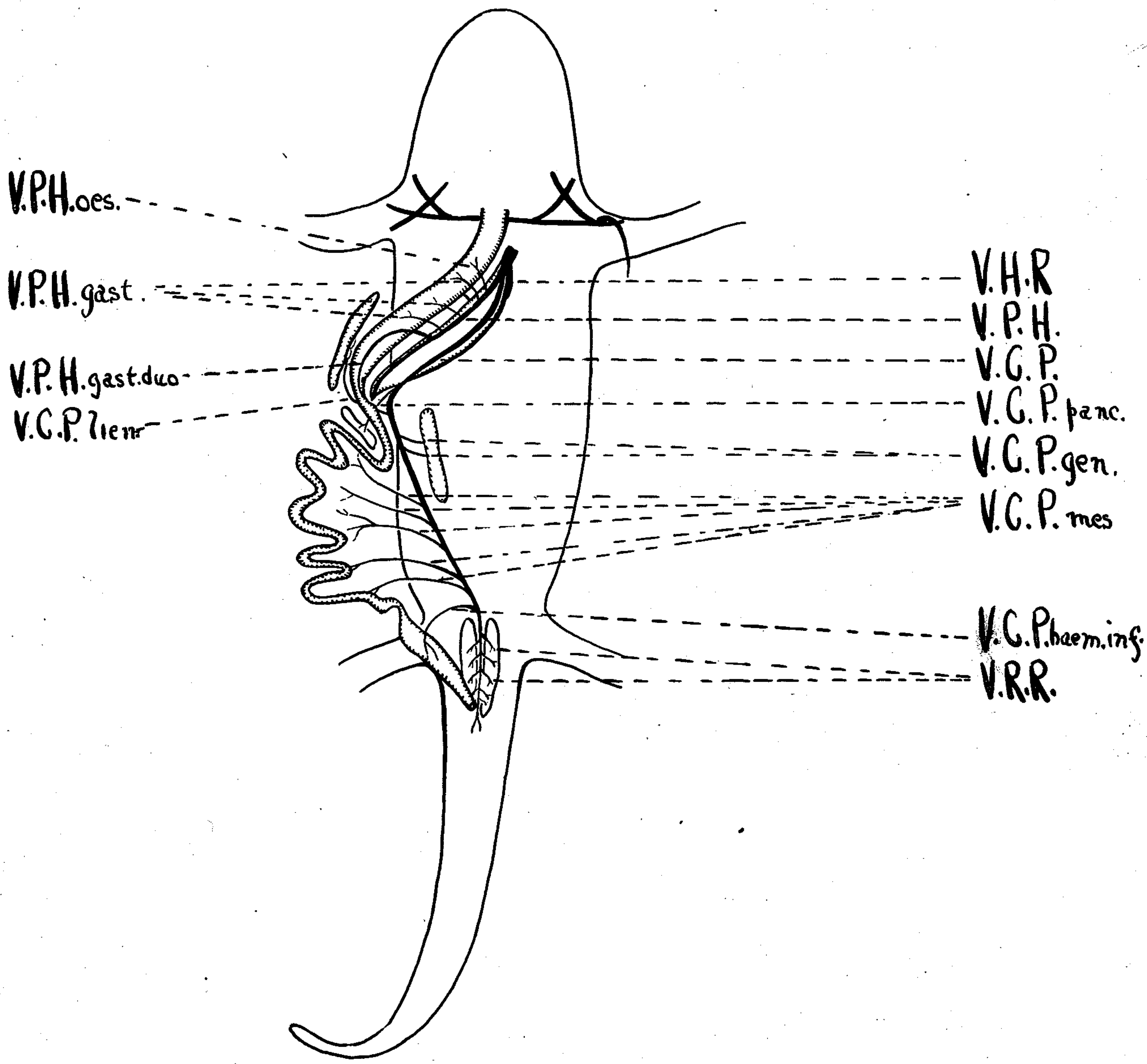

Fig. 9. The Postcaval Venous System. (X.$\frac{1}{3}$)