



CHICAGO JOURNALS



Anatomy of *Cryptobranchus allegheniensis*

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Source: *The American Naturalist*, Vol. 40, No. 472 Apr., 1906), pp. 287-326

Published by: The University of Chicago Press for [The American Society of Naturalists](#)

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ANATOMY OF *CRYPTOBRANCHUS ALLE-* *GHENIENSIS*

ALBERT M. REESE

THE SKELETON

The Skull

SINCE the skull of *Cryptobranchus allegheniensis* is strong and largely composed of bone, it is easy to prepare and to study. Figs. 1 and 2, A and B, are dorsal and ventral views of the skull proper and of the lower jaw, taken from photographs.

The skull as a whole has essentially the same structure as that of the Japanese giant salamander, described and figured by Osawa (: 02), but it differs from the latter somewhat in general outline and in the shape of some of its constituent bones. Its length is greater in proportion to its width than is the case with the Japanese species, and the anterior outline of the head, formed by the maxillary and premaxillary bones, is more rounded in the American species, in which it forms an almost perfect arc of a circle. In the Japanese form the maxilla and premaxilla, as figured by Osawa, are relatively heavier than in the American species, and the posterior ends of the maxillary bones approach more closely the anterior borders of the pterygoids. The shape of the lower jaw is about the same in both species, but, if anything, is narrower in the American salamander, so that it does not fit with very great precision against the upper jaw. The anterior border of the skull is formed, as has been said, by the maxillary and premaxillary bones (Figs. 1, 2, 3, *Mx.*, *P. Mx.*), both of which are armed with numerous small, conical teeth, there being about 12 on each premaxilla, and 38 on each maxilla, making 100 teeth in the entire row.

The cartilaginous portions of the skull are not so extensive as in the Japanese salamander, and are superficially visible in the region of the anterior nares only, the anterior part of the orbit, the auditory region, and the articular surface of the quadrate.

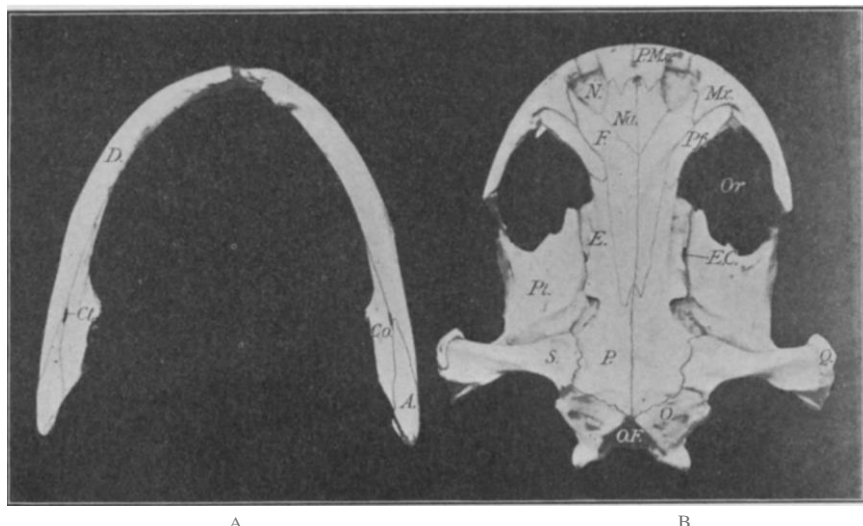


FIG. 1.-A. Ventral view of the mandible. B. Dorsal view of the skull (from a photograph). *A.*, angular; *Co.*, coronoid; *Ct.*, opening of canal ("canalis corde tympani"); *D.*, dentary; *E.*, ethmoid; *E. C.*, ethmoidal canal; *F.*, frontal; *Mx.*, maxillary; *N.*, anterior na.res; *Na.*, nasal; *O.*, exoccipital; *O. F.*, occipital fora.men; *Or.*, orbit; *P.*, parietal; *Pt.*, pterygoid; *P. Mx.*, premaxilla.ry; *Q.*, quadrate; *S.*, squamosal.

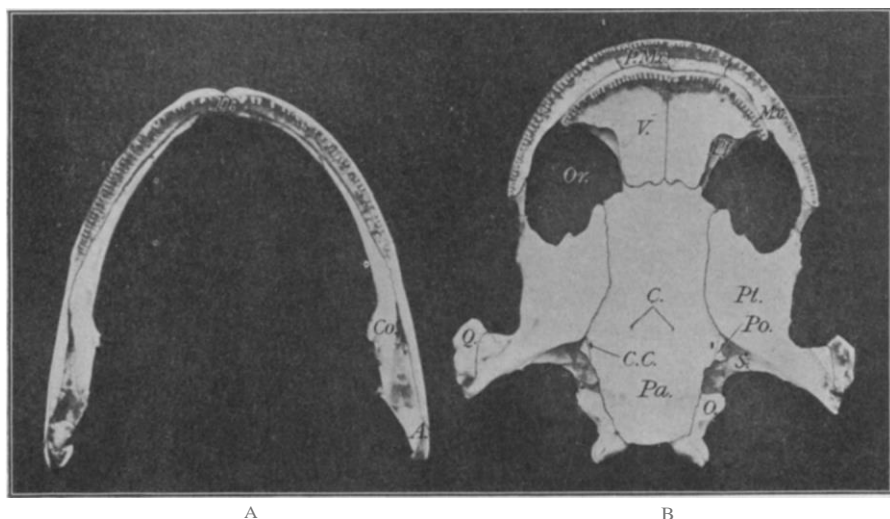


FIG. 2.-A. Dorsal view of mandible. B. Ventral view of skull (from a photograph). *A.*, angular; *C.*, minute canals through parasphenoid; *C. C.*, carotid canal; *Co.*, coronoid; *D.*, dentary; *Mx.*, maxillary; *O.*, exoccipital; *Or.*, orbit; *Pa.*, parasphenoid; *P. Mx.*, premaxilla.ry; *Po.*, prootic; *Pt.*, pterygoid; *Q.*, quadrate; *S.*, squamosal; *V.*, vomer.

The bony cranium will first be described, and then a brief description of the cartilaginous cranium will be given.

The *premaxillae*, forming the extreme anterior tip of the skull, are firmly united with each other in the middle line, and articulate less closely, on each side, with the adjacent maxilla. Their dorsal surface is prolonged backward somewhat, to articulate with the anterior borders of the nasals. Between them, in the mid-dorsal line, is a small foramen, and each of them exhibits a small foramen on its anterior surface (Fig. 1, P. Mx.). Their antero-ventral border is armed with the teeth above mentioned, while the postero-ventral border articulates with the anterior border of the vomers

{Fig. 2, P. Mx., V.}. About half of the median border of the nasal opening (N.) is formed by the premaxilla.

The two *maxillary* bones (*Mx.*) form the rest of the upper jaws, and make up, in fact, about three fourths of their extent. Their entire ventral border is armed, as has been described, with a single row of teeth. The medial end of their arc is in articulation with the premaxillary, while the lateral end tapers somewhat and is connected with the anterior angle of the pterygoid by a tough band of connective tissue. On the dorsal aspect of the maxillary, near the medial end, a triangular projection extends in a postero-medial direction between the frontal and the prefrontal. On the anterior border of each maxilla, at the base of the triangular projection just described, are two small openings, the infra-orbital foramina.

The *nasals* (Figs. 1 and 3, *Na.*) lie just back of the premaxilla and form the posterior half of the median border of the anterior nares (J.V.). The two bones, when taken together, have somewhat the shape of an arrowhead, the tip of the head pointing towards the base of the skull. The base of the arrowhead articulates anteriorly with the posterior projections of the premaxilla that have already been mentioned. In the mid-dorsal line the two nasals articulate closely with each other, while their postero-lateral borders articulate with the frontal bones. The anterior half of each nasal is closely united, ventrally, with the dorsal side of the corresponding vomer, and thus helps to form the septum between the two nasal chambers.

The *frontals* (*F.*) are two large, much elongated bones that lie

just posterior to the nasals and form a considerable part of the roof of the skull. Like the nasals, these two bones, when taken together, have somewhat the shape of an arrowhead, the tip of the head again being towards the posterior. Along the middle line, where the bones articulate with each other, is sometimes seen a well marked ridge. Each frontal forms the posterior half of the lateral border of the corresponding nasal opening, and articulates laterally with the maxillary, prefrontal, and parietal; anteriorly with the nasal, and medially with its fellow of the opposite side. Ventrally the frontals are more or less closely united with part of the cartilaginous cranium, to be described later.

The *prefrontals* (*Pf.*) are two elongated bones in the roof of the skull, on the antero-medial border of the orbits. Each bone articulates anteriorly with the corresponding maxilla, medially with the frontal, and posteriorly with the extreme anterior end of the parietal.

The *parietals* (*P.*) are two large bones that form the greater part of the roof of the cranial cavity. The posterior half of each bone is broad and angular, while the anterior half is long and narrow, and extends forward to articulate with the posterior end of the prefrontal, as has already been stated. The posterior halves of the two parietals articulate with each other, but the narrow anterior portions are separated from each other, and into the space thus formed the posterior ends of the two frontals project and articulate. The narrow, anterior part of the parietal overlies and is more or less closely attached to the ethmoid, presently to be described. The broad, posterior part of the parietal articulates laterally with the squamosal, and posteriorly with the lateral occipital. The sagittal suture, between the two parietal bones, extends back to the antero-dorsal border of the foramen magnum. A very small portion of this border is formed by the medio-posterior extremities of the parietals.

The *ethmoids* (*E.*) will be described at this place, although they are partially composed of cartilage even in the adult, and are described by Osawa in connection with the cartilaginous cranium. The ossified portion of the ethmoid is shown at *E.* in Figs. 1 and 3. It is an elongated rod of bone, attached dorsally to the parietal, as has been mentioned, and ventrally to the parasphenoid

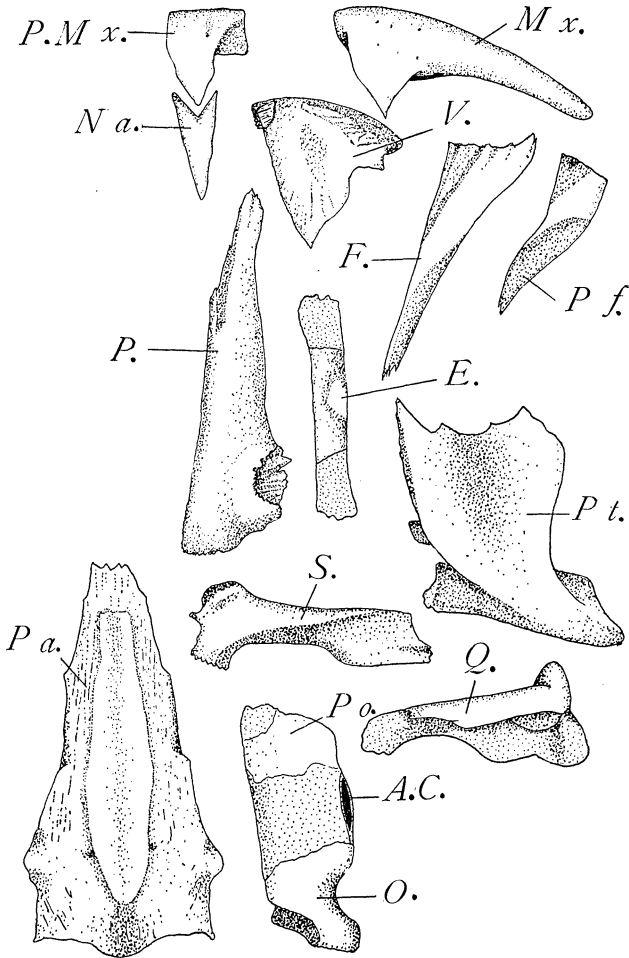


FIG. 3.—The bones of the skull III, disarticulated. A. C., opening of the auditory capsule; E., ethmoid (cartilaginous at each end); F., frontal; *ilx.*, maxillary; Na., nasal; O., exoccipital; P., parietal; Pa., parasphenoid; Pf., prefrontal; *ilfx.*, premaxillary; Po., prootic; Pt., pterygoid; Q., quadrate; S., squamosal; V., vainer.

and, slightly, to the pterygoid. Extending laterally through the midventral region of this osseous part of the ethmoid is a small ethmoidal canal (E. C.). Anteriorly and posteriorly the osseous ethmoid is continuous with the cartilaginous cranium of the nasal and the occipital regions.

The *pterygoid* (Pt.) has, with the exception of the parasphenoid,

a greater surface than any bone in the skull. Seen from the dorsal aspect, it is nearly rectangular in outline, but seen from the ventral side, it exhibits a long, postero-laterally projecting process which underlies the squamosal and quadrate bones. Its anterior and lateral borders are thin, and the former makes the irregular outline of the posterior border of the orbit. The antero-lateral corner is connected with the maxillary by a band of connective tissue, as has already been pointed out. The median border underlies the ethmoid to a slight extent, and is attached ventrally to the side of the parasphenoid. The posterior border is hidden, in a dorsal view, by the squamosal and quadrate, with which it articulates. The above-mentioned postero-laterally projecting process of the pterygoid is an elongation of the lateral and posterior borders, and extends entirely across the squamosal until it shows behind it, and forms a part of the articular surface for the lower jaw. This projection of the pterygoid behind the squamosal and quadrate is shown in Fig. 1. The pterygoid is somewhat arched from side to side, with the convexity of the arch dorsad. Above the postero-median corner of the pterygoid, in the angle between the ethmoid, the parietal, and the squamous, is a marked depression (see Fig. 1) covered in life by a membrane. In the bottom of this depression several canals leading into the cranial cavity may be seen. One of these canals is much larger than the others, and is said by Osawa to be for the exit of the trigeminal nerve. At the postero-lateral corner of the depression is a short canal, formed by a narrow space left between the squamosal above and the pterygoid below. This canal does not lead into the cavity of the skull, but extends backward to the outer side of the auditory capsule, and seems to be an anterior continuation of the vertebral canal; it is apparently the canal that Osawa calls the palatine.

The *squamous* bones (S.) are among the most important in determining the shape of the skull. They are elongated, rod-shaped bones that extend laterally, at right angles to the long axis of the skull, and form the square outline of its base. Each bone has the appearance of being slightly twisted, due to a well marked dorsal ridge that extends nearly its entire length. The medial end of the bone is somewhat flattened and enlarged, and articulates with the side of the parietal near its posterior end.

The distal end of the squamosal is firmly united with the enlarged end of the quadrate, and partially overlies that bone. Ventrally the squamous articulates with the posterior border of the pterygoicl as has been described.

The *quacrate bones* (*Q.*) are two small bones that form almost the entire articular surfaces for the lower jaw. A small portion of these surfaces, however, is formed by the pterygoicls. Each quacrate is a small, triangular bone lying at the distal end of the squamous above described, and largely covered by it. The heavy, basal portion of the bone projects beyond the end of the squamous and, together with the tip of the pterygoicl, is covered with a thick pad of cartilage for articulation with the lower jaw. The slender, medially projecting portion of the bone lies anterior and ventral to the squamous, and dorsal to the pterygoid. It is more closely attached to the former than to the latter bone. Osawa figures the quadrate in the adult skull as entirely of cartilage, and describes it with the cartilaginous cranium, but in the present form it is quite fully ossified.

The *tympanic bones*, described by Osawa in the Japanese species, could not be determined.

The *exoccipitals* (*O.*) form the greater part of the border of the occipital foramen. Each bone presents a postero-laterally projecting condyle, for articulation with the first vertebra. Through the base of this condyle passes a horizontal canal of considerable size into the posterior part of the cranial cavity. This canal is probably for the exit of the vagus nerve. The anterior part of the exoccipital is much enlarged and is hollowed out to form the posterior half of the auditory capsule. The dorso-anterior borders of the exoccipital articulate with the posterior end of the parietal, while the ventral border articulates with the posterior end of the parasphenoid.

The *occipital foramen* or foramen magnum is markedly triangular in outline, especially when seen from the dorsal aspect. The apex of the triangle, which lies at the posterior end of the sagittal suture, is some distance in front of the base, so that the plane of the aperture, instead of being vertical, slants in a dorso-anterior direction. Only a small portion of the base or ventral border of the foramen is formed by the parasphenoid.

All of the bones described above are seen in a dorsal view of the skull; those of the bony cranium that will now be described, are best seen from the ventral aspect.

The *parasphenoid* (*Pa.*) is the only unpaired bone in the skull, and is larger than any other single bone. It forms practically the entire floor of the cranial cavity, as seen from the exterior. The bone as a whole has somewhat the shape of a broad, blunt-pointed dagger, with the point towards the anterior end of the skull, and partially concealed, in a ventral view, by the posterior ends of the vomers, with which it articulates (*Pa.* in Figs. 2 and 3). Laterally the parasphenoid articulates, for the anterior half of its length, with the pterygoids. Just posterior to the pterygoids it articulates dorsally with the small prootics, and posterior to the auditory foramen it articulates with the exoccipitals. Its extreme posterior end forms the ventral border of the occipital foramen. A short distance anterior to this point is seen, in some specimens, a well defined, irregular transverse line (Fig. 2), which would seem to indicate the presence of a basioccipital bone, but as no separation of the bone along this line could be effected, the presence of a definite basioccipital could not be determined. On each side of the parasphenoid, close to its point of union with the prootic, is a canal (*C. C.*), leading into the cranial cavity, called by Osawa the carotid canal. Nearer the midventral line, somewhat anterior to the preceding, are two very small openings (*O.*), probably for the entrance of minute blood vessels. The ventral surface of the parasphenoid is smooth and nearly flat, except at the anterior end where it is more or less convex, with a slight median ridge that fits in between the posterior ends of the vomers.

The *vomers* (*V.*) are the large flat bones that form the base of the anterior end of the skull and the floor of the nasal cavity. They may, perhaps, be considered as formed of the fused vomers and palatines. Each bone is roughly triangular in outline, one side of the triangle being fused with the corresponding side of the other bone in the midventral line. Another side, which is rather deeply indented by a sort of bay, forms part of the inner border of the orbital space; and the third side, which is in the form of an arc and is armed with teeth, is attached to the maxilla and premaxilla. The row of teeth, lying on anterior borders of the two vomers,

forms an arc that is almost exactly concentric with the arc of the premaxillre and maxillre, except that there is a slight depression in the middle where the two vomers meet. The anterior half of the median edge of each vomer is elevated dorsally into a ridge, and the median elevation formed by the union of these ridges separates the nasal chamber into its two parts, and unites the vomers below with the nasals and the premaxillre above. It forms, in other words, the bony nasal septum.

The *prootics* (*Po.*) are two small bones of irregular shape that form the antero-dorsal borders of the auditory capsules. Even in the adult they are largely composed of cartilage, so that in the dried skull they scarcely show from either the dorsal or the ventral side. They are more closely united to the parasphenoid than to any other bone, but they also articulate with the cartilaginous posterior end of the ethmoid, with the parietals, with the squamous bones, and, possibly to a slight extent with the pterygoicls. There are several canals that lead from the exterior to the cranial cavity, in the neighborhood of the prootic. Of these the largest has already been mentioned in connection with the pterygoid bone, and is said by Osawa to be the trigeminal foramen. It is a break in the median border of the prootic, rather than an actual canal through the bone. The only other canal in this bone that can be made out without difficulty is the facial, which lies in the edge of the bony part of the prootic, just dorsal to the carotid canal, and runs transversely through the bone to the cranial cavity.

Colitmella auris is the name given to two very small bones that are found in connection with the auditory capsules. Each columella is fan-shaped or palmate in outline, and, on account of its minute size and loose attachment to the rest of the skull, is easily lost in the preparation of the skull. The broad part of the bone is connected by cartilage with the foramen ovale of the auditory capsule, while the narrow end (the handle of the fan) projects laterally and, according to Osawa, is connected by cartilage with the quadrate, though this latter point could not be determined in the present species. The columella does not show in either of the figures of the skull.

The cartilaginous cranium will now be described. It may be divided, to use the terms adopted by Osawa, into two general

regions, an anterior naso-ethmoidal and a posterior petroso- occipital, regions which are connected by two narrow longitudinal bands in the position of the ethmoids. The space between these bands is the pituitary space, and the bands themselves are ossified in their middle regions to form what we have already described as the ethmoid bones, while their ends are cartilaginous to connect anteriorly and posteriorly with the naso-ethmoid and petroso- occipital regions respectively.

The *naso-ethmoid cartilage* serves chiefly as a lining to the nasal chamber, and may be seen in a dorsal view of the skull, over a part of the anterior nares and at the antero-lateral angle of the orbital space.

The *petroso-occipital* region is more extensive, and the cartilage is there thicker than in the naso-ethmoidal region. It forms, as the name would suggest, the cartilaginous basis of the occipital region, and though in the adult it is largely ossified, there is a considerable cartilage that persists even in the adult skull. The thickest cartilage is found in the region of the ear, where it forms a large part of the auditory capsule. Various parts of the petroso- occipital region are more or less fully ossified to form the following bones, whose form and position have already been described, and which are described by Osawa in connection with the cartilaginous cranium: the exoccipital (occipitale laterale), the prootic, the quadrate, and the columella. The ethmoid,' which forms the middle of the longitudinal bands connecting the petroso-occipital and naso-ethmoidal regions, has also been described in connection with the bony cranium.

It remains now to describe the bones and the cartilages of the visceral skeleton.

The Visceral Skeleton

The *visceral skeleton* is made up of six arches: the mandibular arch or lower jaw, the hyoid arch, and four visceral arches. It differs, then, markedly from the Japanese species which, according to Osawa, has only four arches, the last two visceral arches being absent. The visceral skeleton as a whole is large and strong and, though consisting largely of cartilage, it persists throughout

life. It forms the supporting framework to the floor of the capacious mouth and throat so important in the process of inspiration.

The *mandible* or lower jaw (Figs. 1, 2, 4) is made up of two distinct parts, joined together anteriorly, in the middle line, by a short ligament of cartilage, the mandibular symphysis. As may be seen from the figures, the curve of the anterior margin of the mandible is not so wide as that of the upper jaw, so that the two jaws do not fit together very closely. Each half of the mandible is made up of three elements: the dentary, the coronoid, and the angular.

The *dentary* (*D.*) is the largest of these three bones, and extends from the symphysis almost to the posterior angle of the jaw. Its anterior end is thick and rounded, while the posterior end is thin and pointed to fit against the outer surface of the angular. The ventro-anterior surface of the dentary is smooth, and is marked by a series of about six small openings, mental foramina, which do not show in either a ventral or a dorsal view of the mandible. The dorso-posterior, or upper-and-inner, border of the dentary is depressed to form a deep alveolar surface, along the outer border of which are situated the small, conical teeth in a single row. There are about forty-five teeth in each dentary. The alveolar surface extends for somewhat more than two thirds of the entire length of the bone, and ends posteriorly at the point where the dentary meets the outer border of the coronoid. The teeth are all of nearly the same size,

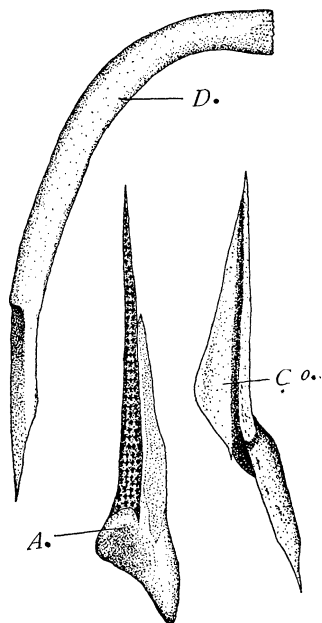


FIG. 4.—The bones of the mandible.. disarticulated. A., angular; Co., coronoid; D., dentary.

except that those at the posterior end of the row are slightly smaller than the rest. They are attached to the bottom and side of the alveolar depression, so that their crowns sometimes project but a short distance above the upper border of the dentary bone..

Individual teeth are frequently broken off, but whether they are ever regenerated again the writer is not able to say.

The *coronoid* (Co.) is a spindle-shaped bone that lies on the inner side of the mandible near its posterior end. Its inner or medial surface is smooth and rounded except near the middle of its length, where it is elevated and roughened to form the coronoid process for the attachment of muscles: In the anterior corner of the triangular depression between the dorsal borders of the dentary and coronoid bones is a small canal leading towards the anterior

•end of the jaw. It may be called the alveolar canal. A ventral view of the jaw shows a more evident canal (Ot.) entering between the dentary and coronoid bones, just at the anterior end of the angular, as seen from the surface but really at some distance behind this end as the anterior portion of the angular is hidden between the two other bones. This canal corresponds, perhaps, to the inferior dental foramen of higher forms. The canal that Osawa describes, in this region, passes directly through the coronoid bone; he calls it the "canalis chordre tympani." The outer surface of the coronoid (hidden, of course, by the other bones) is deeply grooved longitudinally to receive a long, slender process of the angular (Fig. 4).

The *angular* (A.) forms the posterior end of the mandible and presents there an articular surface for attachment to the quadrate. This articular surface is triangular in outline, with the apex of the triangle towards the posterior. The articular portion of the angular is a thick mass of cartilage, and extends forward to fill the angular space between the dentary and coronoid bones that has already been mentioned. Anterior to this angular space, this cartilage is continued forward as a long, slender rod (Meckel's cartilage) lying in a furrow between the dentary and the coronoid. Meckel's cartilage extends for nearly three fourths of the length of the jaw, or to about the middle of the row of teeth. The part of the angular that is seen from the ventral aspect (Fig. 1, A) is ossified, and extends, as may be seen from the figure, for some distance, anteriorly, between the dentary and the coronoid. In fact it extends farther in an anterior direction than is seen from the surface, being covered for some distance by the coronoid.

The *hyoid apparatus* (Fig. 5), using that term to include both

the hyoid and the visceral arches, has, as may be seen from the figure, a very complicated structure. It differs from the same apparatus in the Japanese salamander in having two more visceral arches, as has been said; also in the relative amounts of bone and cartilage, and in the general form of the constituent parts. The arches will now be described in order, from before backward.

The *hyoZ:d arch* (*H.*, *H'*, *C.*) is, as would be expected, much the largest of the arches, and is composed of two S-shaped bars united medially by a smaU, unpaired copula (*C.*). Each bar is made up of two closely united segments (***H.***, ***H'***), of which the anterior one (***H'***) is nearly straight and is united with the copula, while the posterior one (***H.***) is strongly curved outwards at its free or posterior end where it ends

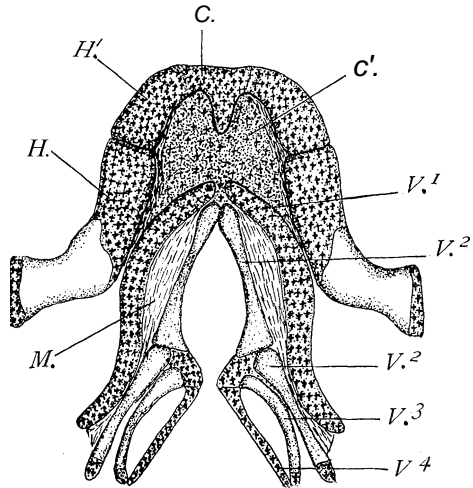


FIG. 5.-The hyoid apparatus. *C.*, copula of hyoid arch; *C'*, copula of first and second visceral arches; *H.*, *H'*, elements of the hyoid arch; *M.*, membrane between the first and second visceral arches; *V.1'* first to fourth visceral arches.

in a cartilaginous surface for articulation with the skull. As may be seen in the figure, nearly half of the posterior segment of the hyoid arch is bony (the cartilaginous portions being, in all cases, clotted). In the Japanese form the entire hyoid arch is composed of cartilage, and each bar is of a single piece, instead of being of two pieces as in the present form. The copula or median connecting piece is of about the same shape in both species, and consists of a short transverse portion with a pointed knob projecting in a postero-dorsal direction. The elements of the hyoid arch are flattened in a dorso-ventral direction, so that they are elliptical in cross section. The whole hyoid arch has somewhat the shape of a wide letter U, with the free ends of the letter bent widely apart. Into the space between the two bars of the hyoid arch projects the

flat, cartilaginous copula (C') of the first and second visceral arches. It is flat, broadly heart-shaped in outline, and is composed of soft, fibro-cartilage. It is united around its periphery with the inner border of the hyoid arch by a thin but tough connective-tissue membrane. On the midventral line of this copula, at its posterior edge, in a slight cartilaginous elevation to which are attached the anterior ends of the first and second visceral arches, the former to its lateral, the latter to its posterior border. The *first visceral arch* (V¹) is composed of two slender, somewhat flattened, S-shaped bars united in the median line by the copula that has already been described. Each bar of this arch is composed of a single rod of firm, translucent cartilage. Along its entire median border this arch is united, by a tough, fibrous membrane, to the outer border of the *second visceral arch* (V²) which, in distinction to the preceding arches, is composed almost entirely of bone. Its constituent bars, instead of being S-shaped, are practically straight laterally though somewhat arched in a dorso-ventral direction. Viewed from the ventral aspect, the two bars of this arch form an almost perfect letter V. Each bar is formed of two elongated bones, of which the anterior or dorsal one is the longer. Both bones are nearly circular in cross section, and are enlarged at each end, the two adjacent ends being the larger, and somewhat flattened. The free end of the posterior or ventral bone is tipped by a small piece of cartilage.

Between the two bones of the second visceral arch, on each side, is a small pad of cartilage which extends medially and becomes spread out for the attachment of the anterior ends of the *third* (V³) and *fourth* (V⁴) *visceral arches*, of which the former is composed almost entirely of bone, and the latter entirely of cartilage. The third and fourth arches are formed of distinct bars; that is, they are not united in the midventral line by a copula as are the preceding arches. The bars of the third and fourth arches on each side are united with each other at both ends, and form a loop which serves to stiffen the border of the permanent gill slit. The third bar is of bone, and is tipped at the posterior end with a small head of cartilage for attachment to the corresponding end of the fourth bar. This bar is cylindrical in cross section, and is slightly curved, so that the loop is kept permanently open, while

the elasticity of the cartilaginous fourth bar allows considerable variation in the size of the loop and consequently in the size of the gill slit. The anterior end of the third bar is united, for a short distance, with the posterior bone of the second bar by the same tough membrane that was noted in connection with the more anterior arches.

The Vertebral Column

The vertebral column of the American salamander (Fig. 6) consists of from 39 to 42 bones or vertebrae. The giant salamander of Japan, according to Osawa, has in its vertebral column forty-five vertebrae, besides two cartilaginous rudiments at the tip of the tail. The vertebrae may be divided into three sets: those of the body, of which there are 19; those of the tail, 19 to 22 in number; and a single vertebra between these two sets, the sacrum. The number of body vertebrae, as might perhaps be expected, seems to be more constant than the number of caudals, though the variation in the latter may be partly due to the great difficulty of preserving the last few vertebrae on account of their small size and cartilaginous nature. All of the vertebral centra, with the exception, of course, of the anterior surface of the first, are deeply amphicelous. The anterior and posterior concavities are so deep that they almost meet in the middle of the centra. There is, however, no continuous passage through the centra.

As a type of the body vertebra, or those lying anterior to the sacrum, the tenth vertebra may be described (Figs. 6 and 7). As is seen in Fig. 7, D, a lateral view, the centrum is distinctly hourglass-shaped, and its length is about twice its greatest diameter.

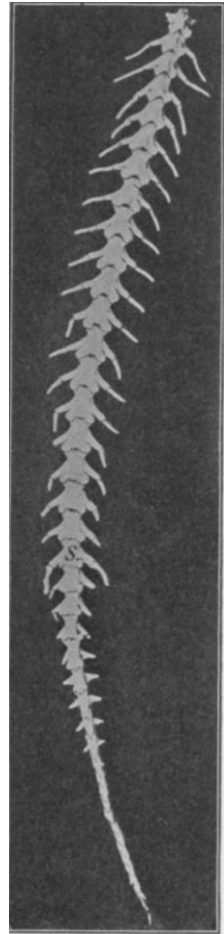


FIG. 6.—Dorsal view of the entire vertebral column, with the ribs attached (from a photograph).

Like all of the other body vertebrae, except the first, this vertebra

has strongly developed transverse processes (Figs. 6, 7, 8, *T.*), to which are attached short, thick ribs (*R.*). These ribs, like the processes to which they are attached, are flattened in an antero-posterior direction, so that, at their points of attachment, they are considerably thicker in a dorso-ventral direction than they are in an antero-posterior direction. The ribs, with the exception of those attached to the sacrum (to be presently described), stand out at right angles from the vertebrae, and taper to a sharp, round point. In the anterior part of the body the ribs are somewhat longer than the processes to which they are attached, while in the region near the sacrum they are shorter. The transverse processes are of about the same length on all of the body vertebrae, and project rather strongly towards the posterior. The base of

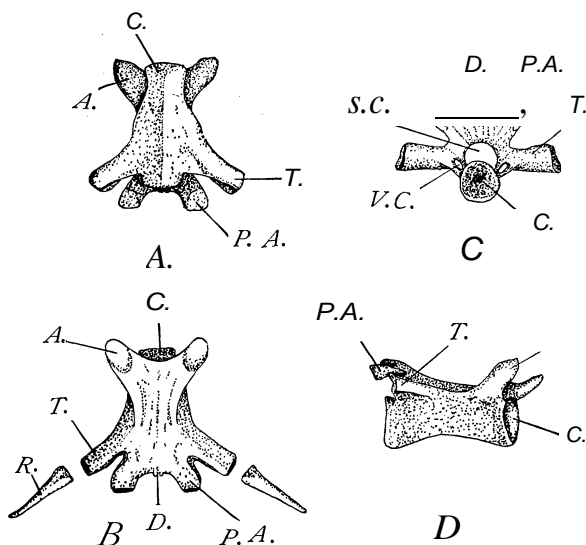


FIG. 7.—Four views of the tenth vertebra. A, Ventral. B, dorsal. C, posterior. D, lateral. A., anterior articular process; C., centrum; D., dorsal spine; P. A., posterior articular process; R., rib; S. C., spinal canal; T., transverse process; V. C., vertebral canal.

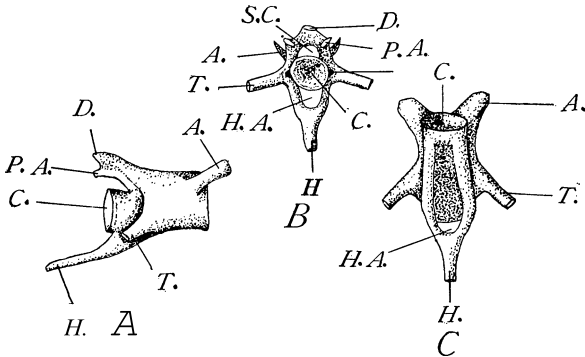
each transverse process is perforated by a small vertebral canal (Fig. 7, *V. O.*). The dorsal or spinous process (Figs. 7 and 8, *D.*) is small and inconspicuous in all of the body vertebrae, and is most prominent on the first.

The posterior articular processes (Fig. 7, *P.A.*) have a rounded outline, as seen from above, and are flattened ventrally where they articulate with the underlying anterior processes of the succeeding vertebra. The anterior articular processes (Fig. 7, *A.*) do not differ greatly from the posterior, except in having their articular surfaces on the dorsal instead of the ventral side. The vertebrae of the body region resemble each other so strongly in shape that it would be very difficult to say from just what part of the body any given vertebra had been taken, but in an individual skeleton the vertebrae in the middle region of the body are both longer and heavier than those anterior and posterior to them.

The sacral vertebra differs from those immediately in front and behind it only in the much greater development of the transverse processes (Fig. 6, *S.*), and the ribs. The sacral ribs, since they serve for the attachment of the pelvic girdle, are much heavier and stronger than any of the other ribs. Instead of projecting as sharp points straight out from the body, they curve downward and end in articular surfaces for the attachment of the upper ends of the two rods of the ilium.

The caudal vertebrae present more variations both in size and form than do those of the body. The first caudal vertebra so closely resembles the last body vertebra that it would be very difficult, if not impossible, to tell them apart. The third caudal vertebra may be described as a type of those of this region (Figs. 6 and 8). The chief differences between this vertebra and the typical body vertebra are, besides the smaller size of the former, the weaker transverse processes, the larger dorsal spine, and the presence of a well developed neural arch. Transverse processes are found on the first eight of these vertebrae, and are provided, at least in the case of the first four or five, with minute ribs. These processes diminish in size from before backward, so that those of the eighth caudal vertebra are very small (Fig. 6). The dorsal spines, on the other hand, become more prominent from before backward, until they reach their greatest development in the mid-caudal region, or, at any rate their greatest relative development. As the caudal vertebrae become more and more compressed laterally, the posterior articular processes approach each other until, in the midcaudal region, they are not distinguishable from the

large dorsal process. Even in the third caudal, these processes (Figs. 6 and 8, *D.*, *P. A.*) have the appearance of being mere articular surfaces on the sides of the spinous process. The anterior articular processes (Figs. 6 and 8, *A.*) also diminish in size towards the posterior until, on the last few vertebrre, they, like the posterior articular processes, practically disappear, and the vertebrre in this region are united by their centra only.



·Fm. 8.-Three views of the third caudal vertebra. A, lateral. B, posterior. C, ventral. A., anterior articular process; C., centrum; D., dorsal spine; H., hremal spine; H. A., hremal arch; P. A., posterior articular process; S. C., spinal canal; T., transverse process.

The hremal arch, which is characteristic of the caudal vertebrre, is well developed on the third vertebra (Fig. 8, *H. A.*), in which the two sides of the arch are prolonged ventrally into a long spine (*H.*). As may be seen in Fig. 8 the canal formed by the hremal arch is larger than the spinal canal; this is true of all the caudals except the first, which is without a hremal arch.

The hinder caudal vertebrre, besides being laterally compressed, show an actual concavity in each side of their centra.

The two cartilaginous rudiments at the end of the tail, that are described by Osawa, I have not been able to determine, though I am not willing to say that they do not exist in the American as well as in the Japanese form. There is, however, except in the number of vertebrre, a strong resemblance between the vertebral columns of the two animals.

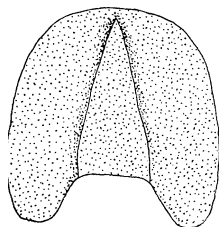
Skeleton of the Appendages

The Anterior Extremity.- Both pairs of appendages are small and weak, and the two girdles are largely made of cartilage. The shoulder girdle is almost entirely composed of cartilage, and the scapular, which is small, is the only part that is bony.

The *sternum* (Fig. 9) is so small and is composed of such thin cartilage that it may easily be overlooked in a hasty dissection.

It lies in the usual midventral position, and is overlapped anteriorly for about half of its length by the large coracoids, that is to say, the coracoids overlap it on its ventral side. In a medium-sized specimen it is about 2.5 centimeters long and of nearly the same width.

It is somewhat shovel-shaped, with the rounded edge toward the anterior (Fig. 9). The ventral aspect is smooth and



Fra. 9.-Dorsal view of the sternum.

slightly convex, while the dorsal side is correspondingly concave, and is provided with a V-shaped thickening, which projects slightly in an antero-dorsal direction. It is chiefly by this thickening that the sternum is attached to the body wall. The edges of the sternum thin out so gradually that it is difficult to determine where the cartilage ends and the fibrous tissue begins.

The *coracoids*, which are described by Osawa as being composed of two parts, the procoracoids (Fig. 10, *P.* 0.) and the coracoids (0.) proper, though there is nothing to distinguish the two regions, are by far the most conspicuous elements of the shoulder girdle. They are composed entirely of cartilage and, together with the sternum, form a complete, though thin cartilaginous sheath for the ventral side of the thoracic region of the body. They overlap each other almost completely, as each sheet extends almost to the opposite side of the body. Like the sternum the coracoid is very thin, especially at the edges, but, unlike the sternum, it has no thickening on either side for muscular or connective tissue attachments. At the outer edge the coracoid becomes considerably thickened, where it articulates with the scapular and with the humerus. With the scapula it is firmly united, but with the humerus it forms a ball-and-socket joint, the glenoid cavity (Fig.

10, *Gl.*) being rather deep to receive the rounded head (*H'*.) of the humerus (*H.*). The center of the coracoid is perforated by an irregular aperture of varying size (*F.*), called by Osawa the "supracoracoid foramen."

The *scapula* and *suprascapula* (Fig. 10, *Sc.*, *S. Sc.*) form, together, a spatula-shaped structure whose area is small in comparison with that of the coracoid, with which it is firmly united. The suprascapula forms the blade of the spatula, and is a broad, thin sheet of cartilage, somewhat curved to conform to the curvature of the side and back of the animal's body. The scapula is.

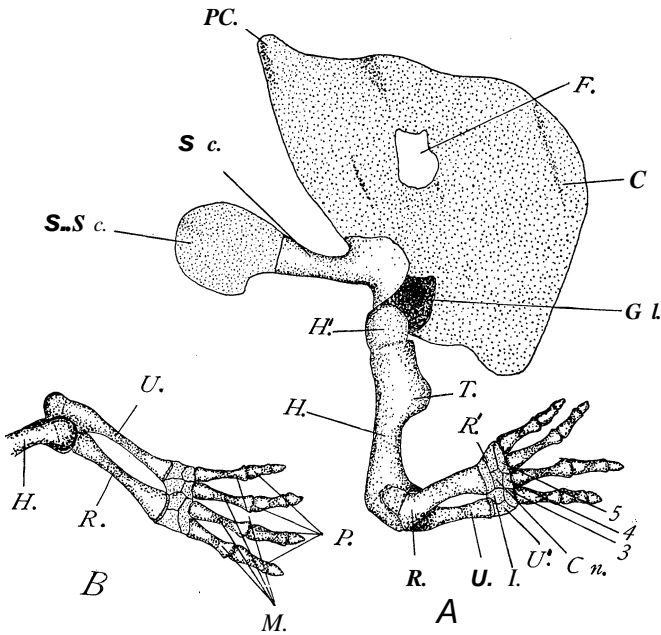


FIG. 10.—Anterior appendage. **A**, entire appendage. **B**, distal portion in a different position. *C.*, coracoid; *Cn.*, centrale; *F.*, foramen; *Gl.*, glenoid cavity; *H.*, humerus; *H'*., head of humerus; *l.*, intermedium; *M.*, metacarpals; *P.*, phalanges; *P.O.*, procoracoid; *R.*, radius; *R'*., radiale; *Sc.*, scapula; *S. Sc.*, suprascapula; *T.*, tuberosity of humerus; *U.*, ulna; *U'*., ulnare; 3, 4, 5, distal row of carpals.

an elongated, somewhat flattened structure, slightly enlarged at one end, where it is attached to the suprascapula, and considerably enlarged at the other, where it is attached to the coracoid. It is the only part of the shoulder girdle that is composed of bone.

The *humerus* (Fig. 10, *H.*) is rather thick in proportion to its.

length, and articulates with the glenoid cavity of the coracoid by the round, cartilaginous head (*H'*). Its more or less cylindrical shaft is marked by a large tuberosity (*T.*) near its proximal end, and is separated from the head by a well marked neck. At its distal end it is broad, somewhat as in the human humerus, and articulates with both the radius and the ulna.

The *radius* and the *ulna* are entirely distinct from each other, and take nearly equal parts in the formation of both elbow and wrist joints, though the ulna, as is usual, is the more closely associated with the humerus. The ulna (Fig. 10, *U.*) is slightly longer than the radius (*R.*), and strongly resembles the corresponding bone in the human arm, though it is, of course, not so long in proportion to its diameter, and its shaft is not so nearly cylindrical in section. Its proximal end is enlarged to form the concave articular surface, the sigmoid cavity, and its distal end is also slightly enlarged, and is provided with a disc of cartilage of considerable thickness. The radius presents no peculiarities in structure. It enlarges rather rapidly from the center towards each end, where well marked discs of cartilage are found.

The *carpus*, though composed entirely of cartilage, shows with considerable distinctness the seven elements of which it is made up. Two elements articulate with each of the forearm bones: on the radial side are the radiale (*R'*) and the centrale (*On.*), the latter lying in about the center of the carpus; on the ulnar side are the ulnare (*U'*) and the intermedium (*I.*) Uniting the four elements above described with the metacarpals are three distal carpals (Fig. 10, 3, 4, 5), one of which is united with two of the metacarpals. On the anterior appendage are four digits, each of which is made up of an elongated metacarpal element (11£.) and two short phalangeal elements (*P.*), of which the more distal tapers to an almost claw-like sharpness. The two middle digits which are of about the same length, are somewhat longer than the two outer ones. There is no sign, on the fourth digit, of the third phalangeal element described by Osawa in the Japanese salamander. The relative sizes of the metacarpal and phalangeal elements are about the same in each of the four digits.

The Posterior Extremity.—The posterior extremity, consisting of the pelvic girdle and the hind legs, is a rather curious mixture

of cartilage and bone. Its structure, in general, agrees closely with the corresponding region in the Japanese species, as described by Osawa, except in regard to the epipubis, which is markedly different.

The *pelvic girdle* will first be described. Taken as a whole, it has a roughly triangular form. The apex is formed by the anteriorly directed epipubis, while the basal angles are formed by the dorso-posteriorly directed ilia. Its ventral surface is somewhat convex, and, along its posterior half, is marked by a slight, median, longitudinal ridge for the attachment of muscles. Its dorsal surface is concave, with the most marked concavity between the bases of the two ilia (Fig. 11). The greater part of the pelvis is made up of the pubis, which is divided into two parts, the pubis proper, and the epipubis.

The *pubis* proper is a shield-shaped plate of cartilage (Fig. 11, P.), whose ventral convexity and dorsal concavity have been mentioned in speaking of the pelvis as a whole. It is almost completely divided into lateral halves by a median suture which is especially evident at the posterior end of the pelvis, between the two ischia (Fig. 11, S.). On each side of this suture, slightly anterior to the middle region, there is a small opening (Fig. 11, O. F.), the obturator foramen. The posterior corners of the pubis are elevated for the attachment of the ilia (/.), and under these elevations the deep, well developed acetabula are situated.

Anteriorly, the pubis is prolonged into a long, cartilaginous *epipubis* (*Ep.*), which, instead of being forked as in the Japanese salamander and some other Amphibia, is a straight rod, slightly broadened and flattened at its distal end and somewhat enlarged both laterally and dorso-ventrally at its attached end. The union of the pubis and epipubis is a close one, but allows considerable freedom of motion.

Firmly united with the posterior end of the pubis, and continuous with it, are two oblong plates of bone, the *ischia* (*Is.*). Together, the ischia form a blunt, posteriorly projecting process to the pelvis. The ischia are separated along the middle line by the median suture, but their adjacent edges are not quite parallel, so that a slight cartilage-filled space is left between them at one place. There is also a small triangular piece of cartilage at their extreme posterior end.

The *ilia* (*I.*), like the ischia, are of bony consistency, except at their extremities, where there is a small amount of cartilage. They are somewhat curved in a postero-dorsal direction, and are considerably enlarged at their pelvic end, and less so at their sacral end.

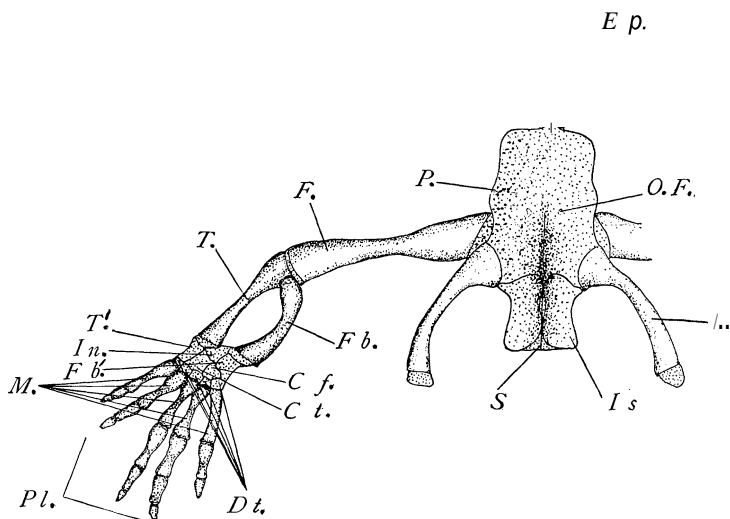


FIG. 11.—Posterior appendage, from the dorsal aspect. *Cf.*, centrale fibulare; *Ct.*, centrale tibialis; *Dt.*, distal row of tarsal elements; *Ep.*, epipubis; *F.*, femur; *Fb.*, fibula; *Fb'*, fibulare; *I.*, ilium; *In.*, intermedium; *Is.*, ischium; *M.*, metatarsus; *O.f.*, obturator foramen; *P.*, pubis; *Pl.*, phalanges; *S.*, suture; *T.*, tibia; *T'*, tibiale.

The *femur* (Fig. 11, *F.*) is rather more slender in proportion to its length than it is in the Japanese animal. Its proximal end is enlarged to form a round, cartilaginous head, which articulates with the deep acetabular cavity that has already been mentioned. On the ventral side, near the proximal end, is a sort of trochanter, or roughened projection for the attachment of muscles. The shaft tapers rapidly from the enlarged proximal end to about the middle length of the bone, where it is nearly cylindrical in cross section, and is not more than half the diameter of the head. The distal half of the femur is much broadened, in a dorso-ventral direction, and flattened in an antero-posterior direction. This marked flattening does not show in the figure because of the posi-

tion in which the leg is drawn. This distal enlargement of the femur is slightly convex on its anterior surface, and concave on its posterior surface. On the convex anterior surface is a very slight ridge, which is prolonged distally as an inconspicuous knob. Almost the entire distal end of the femur articulates with the tibia, but there is a small articular surface for the proximal end of the fibula. Between the distal end of the femur and the proximal ends of the tibia and fibula is a layer of cartilage of considerable thickness.

The lower leg is made up of two entirely distinct bones, the tibia and fibula. Of these bones, the tibia (Fig. 11, *T.*) is larger and will be described first. It is considerably larger at its proximal than at its distal end, and forms almost the entire articular surface of the knee-joint. The proximal end is broadened and flattened in the same planes as is the distal end of the femur, with which it articulates. On the anterior surface of this end is a slight ridge, corresponding to the ridge that has been noted on the distal end of the femur. The shaft of the tibia tapers rapidly from the proximal end to a point a little beyond the middle of the bone, and then increases in size to form the somewhat flattened distal enlargement, which articulates with the tibiale and centrale of the foot. The flattening of the distal end is in the same plane as that of the more enlarged proximal end. The distal, like the proximal end, is provided with a well developed plate of cartilage.

The *fibula* (Fig. 11, *Fb.*) is not so long as the tibia, and, as is shown slightly exaggerated in the figure, is strongly bowed on the tibial side. The side away from the tibia is only slightly bent, so that the bow is chiefly due to the shape of the surface next to the tibia. The enlargement at the proximal end is rounded, and articulates laterally with the side of the tibia and proximally with the distal end of the femur. The shaft of the bone is somewhat flattened, so that it is elliptical instead of circular in cross section. The distal end is more enlarged than the proximal, but is flattened instead of being rounded. At the extreme end of each flattened surface is an inconspicuous depression, not shown in the figure. The fibula, like most of the other bones that have been described, ends, both proximally and distally, in cartilage.

The *tarsus*, like that of the Japanese species, is composed of

ten cartilaginous elements, which are arranged in two more or less definite groups, the proximal and the distal, with two elements in an intermediate position. Articulating with the tibia, or rather with the cartilage that tips the distal end of the tibia, is the *tibiale*, (*T.*) an irregular, elongated mass of cartilage. Attached in the same way to the fibula is the *fibulare* (*Fb.*); and lying in an intermediate position and articulating more or less with tibia, fibula, tibiale, and fibulare is the angular *Intermedius* (*In.*). The distal row of tarsal elements (*Dt.*) is composed of five masses of cartilage, all of about the same size, and each attached to the basal end of one of the metatarsal bones. These distal cartilages are smaller than the proximal. Between the proximal and the distal rows, are two small elements (sometimes fused into one) called by Osawa the "*centrale tibiale*" and "*centrale fibulare*" (*Ct.* and *Cf.*).

The *metatarsus* (111.) is composed of five elongated, cylindrical bones, somewhat enlarged as usual at the ends. They are of nearly the same length, though the first (on the tibial side) is somewhat shorter than the rest, and the third and fourth are somewhat longer.

The *phalanges* (*Pl.*) of the first, second, and fifth digits are made up of two elements, while those of the third and fourth digits contain three elements each. The terminal element of each digit is a pointed, claw-like structure.

Tern VASCULAR SYSTEM

For the purpose of working out the course of the blood vessels the usual method of injecting the arterial and venous systems with masses of different colors was used. The injection of the arterial system was accomplished with but little difficulty by inserting the cannula into the well developed conus arteriosus, and through it forcing the injection mass into all of the arteries. But the injection of the veins was a more difficult matter, and will be described in connection with the description of those vessels.

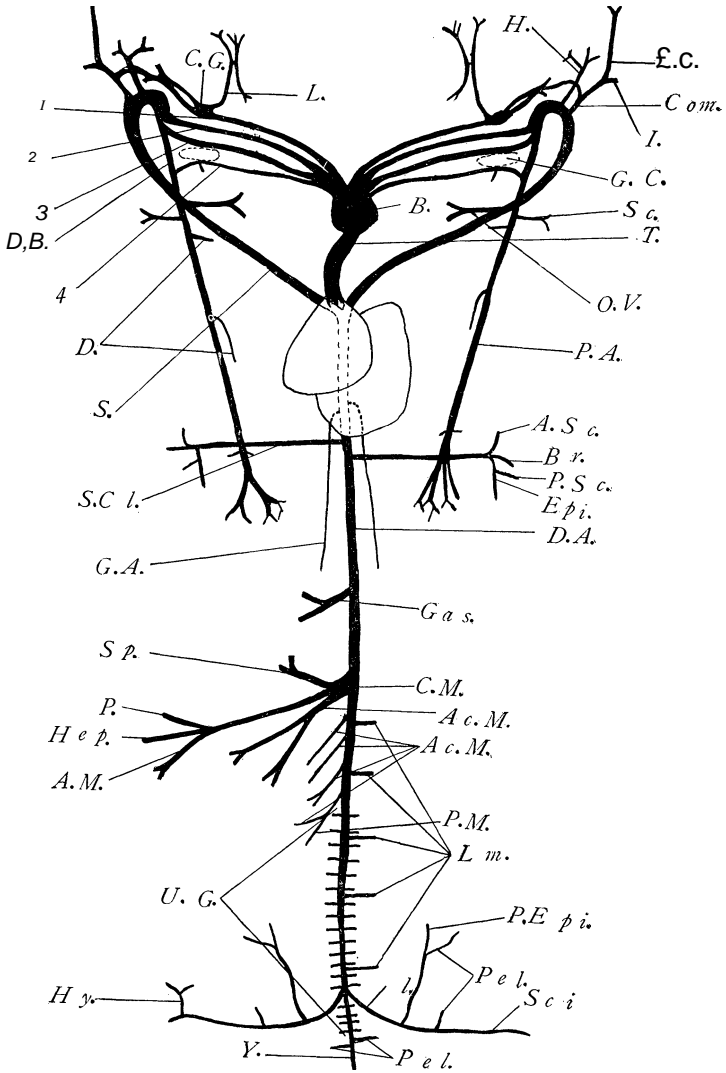
The Arterial System

From the anterior edge of the ventricle leads forward the thick-walled conus arteriosus (Fig. 12, *T.*). It is of considerable length, and is more or less bent towards the right. It becomes considerably enlarged anteriorly to form the conspicuous bulbus arteriosus (*B.*). The bulbus arteriosus gives off from its anterior end, on each side, four branchial vessels (Fig. 12, 1, 2, 3, 4), which diverge slightly as they pass towards the side. All four of these arches are united with one another, just beyond the gill cleft (*G. O.*), but it is from the second and third that the real systemic arch (*S.*), is chiefly formed. This complicated arrangement of the branchial blood vessels is, in the main, similar to that described in the Japanese hellbender by Osawa, but differs considerably from the description given by Chapman ('93), also of the Japanese salamander.

The first arch, which may be called the *carotid*, extends for some distance as a single vessel and then becomes slightly swollen to form a sort of *carotid gland* (*C. G.*), similar to that found in the frog. From the median side of the carotid gland is given off an artery which is distributed to the hyoid apparatus and the floor of the mouth, and may hence be called the *lingual* (*L.*).

Just beyond the carotid gland the arch divides and reunites again, giving off one or two small vessels to the neighboring parts. Then, after continuing for some distance as a single vessel, it divides into two vessels, the *external* and *internal carotids* (*E. C., I.*). Just before dividing into the external and internal carotids the arch is connected with the main systemic arch by a vessel that is called by Marshall the ductus Botalli, by Osawa the ramus communicans (*Com.*).

The *second* and *third branchial arches* (Fig. 12, 2, 3), after running more or less parallel to each other to a point back of the carotid gland, unite to form the main *systemic arch* (*S.*). The third arch runs along the anterior margin of the gill cleft (*G. O.*), and gives off, just before uniting with the second arch, a branch to the fourth branchial arch. This branch may be called the ductus Botalli (*D. B.*).



Fm. 12.-The arterial system, ventral aspect. *A. l'of.*, anterior mesenteric; *Ac. M.*, accessory mesenteric; *A. Sc.*, anterior scapular; *B.*, bulbus arteriosus; *Br.*, brachia; *C. G.*, carotid gland; *C. 1y.*, ceeliaco-mesenteric; *Com.*, ramus communicans; *D.*, to dorsal region, near lungs; *D. A.*, dorsal aorta; *D. B.*, ductus Botalli; *E. C.*, external carotid; *Epi.*, epigastric; *G. A.*, anterior genital; *Gas.*, gastric; *G. C.*, gill cleft; *H.*, hyoid; *Hep.*, hepatic; *Hy.*, hypogastric; *I.*, internal carotid; *Il.*, iliac; *L.*, lingual; *Lm.*, lumbar; *O. V.*, occipito-vertebral; *P.*, pancreatic; *P. A.*, pulmonary; *Pel.*, pelvic; *P. Epi.*, posterior epigastric; *P. M.*, posterior mesenteric; *P. Sc.*, posterior scapular; *S.*, systemic arch; *Sc.*, scapular; *Sci.*, sciatic; *S. Cl.*, st\bclavian; *Sp.*, splenic; *T.*, conus arteriosus; *U. G.*, urogenital; *Y.*, caudal; 1, 2, 3, 4, first to fourth branchial arches.

A short distance beyond the point of union of the second and third arches, the systemic arch gives off a well marked vessel (*H.*), to the end of the hyoid apparatus, and some distance beyond this it gives off an occipito-vertebral artery to the vertebral column and occipital region (*O. V.*). After passing around to the dorsal side of the digestive tract, the two systemic arches unite, just above the heart, to form the dorsal aorta (*D. A.*).

The *fourth branchial arch* passes just posterior to the gill opening, at the outer margin of which it is connected with the third arch by the ductus Botalli. Beyond the ductus Botalli it gives off an artery (*Sc.*) to the region of the scapula, and then two small arteries (*D.*) to the muscles of the dorsal part of the body in the region of the lungs. The main branch of this arch continues posteriorly as the pulmonary artery (*P.A.*).

Some variation in the relative sizes of the vessels of the branchial region occurs as well as some slight variation in their distribution, but the normal condition is about as described above.

The distribution of the blood vessels that arise as branches of the dorsal aorta will now be described. The aorta and its branches are so easily filled with the injection fluid that it is a comparatively easy matter to work out their distribution, especially in the abdominal region. In fact, the only part of the arterial system that offers any difficulty is the outer part of the visceral arches, in the region of the gill openings.

The branches of the aorta will be described in order from before backward. The most anterior branches are given off in the region of the heart, as a pair of rather small arteries (Fig. 12, *G. A.*) which arise nearly opposite each other and extend in a posterior direction to supply the anterior part of the reproductive organs, especially the oviducts.

A short distance posterior to the last described arteries, are given off the two *subclavians* (*S. Cl.*), the right vessel arising a little anterior to the left. As might be expected from the slight development of the anterior appendages, the subclavian arteries are comparatively small vessels. On reaching the shoulder girdle, each subclavian divides into four main branches. The most anterior of these (*A. Sc.*) supplies blood to the region in front of the scapula. The next branch (*Br.*) is the brachial, and extends

into the fore leg. The third branch (*P. Sc.*) extends to the region posterior to the scapula, and also probably, to the posterior border of the fore leg. The most posterior branch of the subclavian (*Epi.*) runs in a posterior direction, and carries blood to the lateral part of the body back of the anterior leg; it is called by Osawa the epigastric.

Some distance posterior to the subclavians is seen an unpaired vessel (*Gas.*) which sends branches to the lesser curvature of the stomach, and may be called the gastric. The next artery, which may be called the cceliaco-mesenteric (*C. JJ1.*), is a rather large one, and branches almost immediately into three parts. The most anterior of these branches (*Sp.*) supplies the greater curvature of the stomach, and also the spleen, and may be called the splenic. The second branch of the cceliaco-mesenteric divides into three smaller branches: a pancreatic (*P.*) supplying the pancreas; a hepatic (*Hep.*) supplying the liver; and a third branch, the anterior mesenteric (*A. M.*), which carries blood to the anterior third of the small intestine.

The most posterior of the three branches of the cceliaco-mesenteric artery is distributed to the small intestine posterior to the region supplied by the anterior mesenteric; it is the first of several vessels that supply blood to the posterior two thirds of the small intestine, and that might be called accessory mesenterics (*Ac. JJ1.*). There are three unpaired accessory mesenterics posterior to the one just described, and a fourth is formed as one of the two divisions of another unpaired branch of the dorsal aorta (*Ac. M.*). There are thus five of the so called accessory mesenteric arteries.

The artery (*P. M.*), with which the most posterior of the accessory mesenterics unites to form a single vessel is the posterior or inferior mesenteric and supplies blood to the anterior third of the large intestine. Five or six rather large, unpaired arteries (*Lm.*) are given off by the aorta, at more or less regular intervals, between the origin of the cceliaco-mesenteric and the iliacs. These lumbar arteries pass into the body wall along the mid-dorsal line. Numerous pairs of urogenital arteries (*U. G.*) are given off by the aorta in the abdominal region, and supply the kidneys and reproductive organs. On account of the great elongation of the kidneys in a posterior direction, the last of the urogenital arteries

lie as far back as the cloaca or even posterior to it. In the neighborhood of the cloaca, the dorsal aorta gives off a pair of large arteries, the iliacs (*Il.*) which are continued into the posterior appendages as the sciatic arteries (*Sci.*). Each iliac artery gives off, a short distance from its origin, a vessel, the posterior epigastric (*P. Epi.*), which is chiefly distributed to the ventral body wall, but which also sends blood to the pelvic region (*Pel.*). A short distance distal to the posterior epigastric, each iliac gives off a small artery to the pelvic region. From the right iliac an additional artery is given off, distal to those just described, to the bladder and the posterior end of the rectum. This is the hypogastric (*Hy.*).

Posterior to the point of origin of the iliac arteries, the aorta continues backward, with diminished caliber, as the caudal artery (*Y.*) to supply blood to the tail. Besides several pairs of renal arteries, there is given off from the aorta, just back of the iliacs, a pair of arteries (*Pel.*), to supply blood to the dorsal region of the pelvis. This completes the description of the more important vessels of the arterial system. Without stopping to describe the distribution of the more minute vessels, the venous system will now be described.

The Venous System

The venous system is much more difficult to work out than the arterial system, due chiefly to the difficulty of obtaining good injections, especially in the region anterior to the heart.

The venous system, as described in this paper, will exhibit more differences from that described by Dr. Osawa for the Japanese giant salamander than were seen in connection with the arterial system. The veins of the posterior region of the body were injected, without especial difficulty, as follows: the abdominal vein was injected both forwards and backwards; the portal vein was injected forwards, beginning so far towards the tail that practically the entire system was filled; and the posterior vena cava was injected by cutting off the tail and inserting the cannula into the caudal vein. The veins of the anterior parts of the body were injected through the anterior venre cavre, and it was here

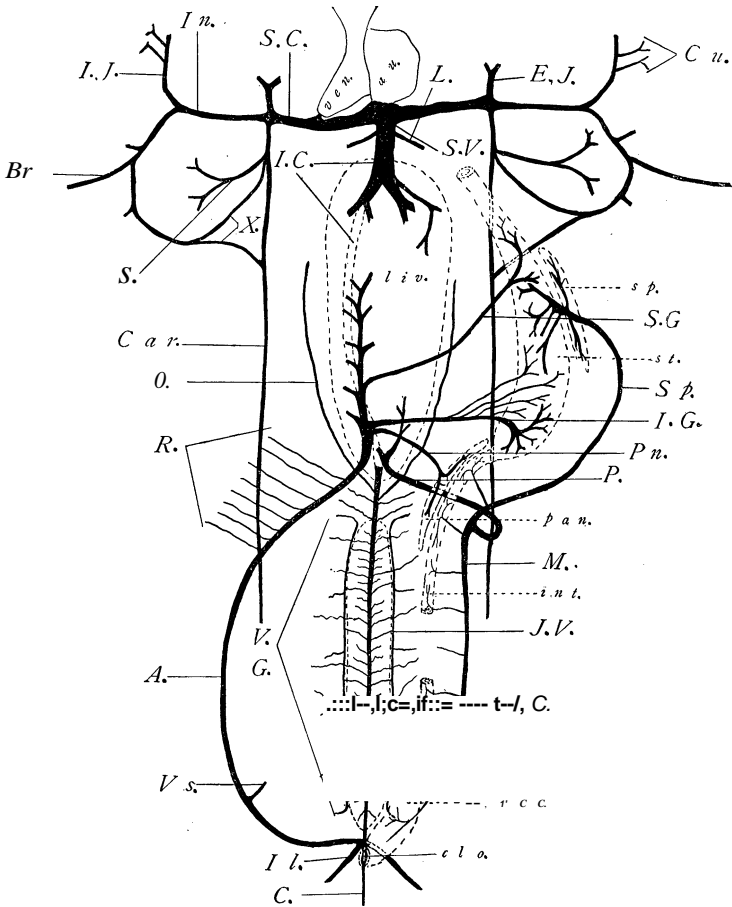
that the greatest difficulty was experienced in getting the injection fluid into the smaller vessels, in fact, it was only by repeated injections at various points that even the more important veins of this region could be filled. The posterior end of the posterior cardinal veins could not be filled with the injection mass, even after repeated attempts, so that the connections of these veins, if any exist, with the other veins of the abdominal region could not be made out.

The conspicuous, thin-walled *sinus venosus* (Figs. 13 and 14, S. V.) into which the blood from the various parts of the body is emptied, is formed mainly by the union of three large veins: the two superior vena cava (S. C.), and the inferior vena cava (I. C.). The pulmonary veins (L.), bringing blood back to the heart from the lungs, as their name would indicate, unite with each other dorsal to the sinus venosus, and empty into the latter at a point whose exact location is difficult to determine on account of the small size of these pulmonary vessels. The superior vena cava of the right side seemed in most, if not all cases, to be attached to the apex of the ventricle. What the object of this attachment might be, was not determined. Each superior vena cava is formed by the union of the following veins: the innominate (In.) which is practically nothing more than the lateral continuation of the superior cava itself, the external jugular (E. J.), and the posterior cardinal (Car.).

The external jugular collects blood chiefly from the lower side of the head, and is formed by the union of two veins which probably correspond to the mandibular and lingual or laryngeal, though they could not be traced to their origin.

The posterior cardinal (Car.) empties into the superior cava at a point nearly opposite the opening of the external jugular. Throughout most of its course it lies deeply buried in the muscles of the dorsal body wall, and, as has been said, its extreme posterior termination could not be determined, owing to the impossibility of obtaining a complete injection. It was traced backward as far as the anterior end of the kidney, but whether beyond that point it is simply lost in the body wall or is connected with some of the veins of the abdominal region, could not be determined. Near its anterior termination the posterior cardinal is

joined by a vessel (S.) from the region of the shoulder, and a short distance posterior to this point it is connected, by a sort



Fro. 13.-The venous system, ventral aspect. A., abdominal; Br., brachial; C., caudal; Car., posterior cardinal; Cu., cutaneous; E. J., external jugular; G., genital; I. C., inferior cava; I. G., inferior gastric; I. J., internal jugular; *ll.*, iliac; In., innominate; J. V., vein of Jacobson; L., pulmonary; M., mesenteric; O., oviduct; P., portal; Pn., pancreatic; R., parietals; S. C., superior vena cava; S., from shoulder; Sp., splenic; S. V., sinus venosus; V., vertebral; Vs., from urinary bladder; X., plexus.

of simple plexus of veins (X.), with the brachial vein (Br.) which brings blood to the heart from the anterior appendage. To the brachial and to the plexus of veins just mentioned, are added a

number of small veins from the region of the shoulder. The innominate vein (*In.*) is formed by the union of the internal jugular (*I. J.*) and the brachial (*Br.*). The main branch of the former returns blood from the interior of the skull, and is joined shortly before its union with the brachial, by two smaller vessels (*Cu.*), leading from the side of the head. The brachial, as might be expected from the small size of the fore leg, is a comparatively small vein. This completes the description of the vessels connected with the superior venre cavre, as the vessels of the two sides of the body in this region are alike.

The veins of the abdominal region will now be described. Since these vessels are usually injected without difficulty, their distribution may be made out with comparative ease. One of the largest and most noticeable veins in the body is the *abdominal (A.)*. It adheres closely to ventral body wall, slightly to the right of the median line, and, unless care be taken, may easily be cut in opening the abdominal cavity. In the diagram it, like the veins from the stomach and intestines, is for the sake of clearness drawn towards the side. Posteriorly it is formed chiefly by the union of the two iliac veins (*Il.*), a union which takes place just anterior to the cloaca (*clo.*). The iliac veins return the blood from the posterior appendages, and, like the brachial veins, are of comparatively small size. A short distance anterior to the point of union of the iliac veins the abdominal vein receives a very small vein (*Vs.*) from the urinary bladder. Into the most anterior quarter of the abdominal vein, near to its junction with the liver, empty several (eight or nine) veins, the parietals (*R.*), which return blood from the ventral body wall. Anteriorly, the abdominal vein enters the liver, a little in front of the apex, and becomes broken up into capillaries, though it may be traced along the ventral surface of the liver for a considerable distance in an anterior direction.

The arrangement of the veins from the stomach and intestines, the *hepatic-portal system*, is rather peculiar, and will now be described. The blood from practically the entire length of the intestines, both small and large, is collected by a single vein (*M.*) which may be called the mesenteric. A short distance posterior to the liver, this vein unites with the splenic vein (*Sp.*) to form the

main branch of the portal vein (*P.*) through which the blood finds its way into the liver. The splenic vein, as its name would indicate, collects blood from the spleen, but it brings blood also from the middle region of the stomach. The greater part of the blood from the stomach is collected into two well marked veins, the superior and inferior gastrics (*S. G.*, *I. G.*) which empty into that part of the abdominal vein which has already been described as extending for some distance along the ventral side of the liver. Of these two gastric veins, the inferior is the larger, and empties into the abdominal vein at some distance behind the superior gastric. Emptying into the abdominal at almost the same place with the inferior gastric, is a vein of considerable size, the pancreatic (*Pn.*). The portal vein proper, then, brings blood to the liver from the intestines and the spleen; but most of the blood from the stomach and apparently all that from the pancreas is

•Carried into the liver through the abdominal vein.

It now remains only to describe the system of the *inferior vena cava*, and especially that part of the system that lies posterior to the liver. The blood from the tail is collected into a caudal vein (*C.*) that, after entering the abdominal cavity, becomes the inferior or posterior vena cava (*I. C.*). This posterior part of the inferior cava lies between and slightly ventral to the kidneys, and is so closely associated with these organs, from which it receives numerous veins, that its individuality as a distinct vessel seems almost lost. Extending along the distal sides of the kidneys, and connected at frequent intervals by small vessels with the inferior cava, are the more or less distinct veins of Jacobson (*J. V.*). Each vein of Jacobson receives about six vertebral veins (*V.*) from the corresponding side of the vertebral column. On account of the great number of the renal veins and the close attachment to the kidneys of the veins of Jacobson, the details of these veins are difficult to determine.

The blood from the reproductive organs is emptied into the inferior cava through several pairs of genital veins (*G.*), some of which lie anterior to the kidneys while some cross the anterior ends of these organs to reach the inferior cava. In the female, a comparatively large vein leads from the anterior end of each oviduct to empty into the inferior cava just behind the liver (*O.*).

The inferior cava enters the liver near the apex of the right lobe. By carefully dissecting away the substance of the liver, the course of this large vein may be followed entirely through that organ. It extends in a nearly straight line through the dorso-lateral part of the right lobe, and emerges from the anterior surface of the liver as the large thin-walled vessel that empties into the heart. Just before, or at about the time of its emergence from the liver, it is joined by the large hepatic vein, so that that part of the inferior vena cava which is anterior to the liver is many times as large as that part which is posterior to the liver. This completes the description of the more important peripheral vessels of the vascular system; and it now remains to describe the structure of the heart.

The Heart

The heart lies far forward in the body, just anterior to a line joining the front legs. It is protected ventrally by the broad underlying cartilages of the procoracoids and the sternum, to which it lies so close that they must be removed with some care in order not to cut into the pericardial cavity. The size of the heart is moderate in relation to the size of the entire animal, and seems to vary considerably, even in animals of the same approximate size. It has the vitality usually seen in cold-blooded animals, and will continue to beat for a considerable time after being removed from the body, or after being filled with the injection fluid.

External Anatomy.- When seen from the ventral aspect (Fig. 14, A), it presents six main regions: the conus arteriosus, the bulbus arteriosus, the ventricle, the right and left atria or auricles, and the sinus venosus. These regions may be seen from the dorsal aspect as well, if the heart be dissected from the body (Fig. 14, B), and they will now be described in turn. Their form and relative size will vary somewhat, of course, with their state of distension at the time they are sketched. The heart from which the figure was made, was moderately well filled with the injection fluid, and differs considerably in general appearance from Osawa's figures of the heart of the Japanese salamander.

The bulbus arteriosus (*B.*), to begin at the most anterior region of the heart, is a striking object, seen on removing the skin and the

cartilages of the pectoral girdle from the ventral side of the throat. It is of a whitish color, and its walls are tough and thick. Anteriorly it divides to form the arterial arches of each side, and posteriorly it narrows suddenly to form the truncus, which connects with it at somewhat of an angle, instead of entering exactly in the middle line. Its ventral surface is smooth and even, while its dorsal surface may be more or less grooved longitudinally, as seen in the figure. In cross section it is elliptical, and is compressed in a dorso-ventral direction.

The conus arteriosus (0.) is a well marked tubular structure

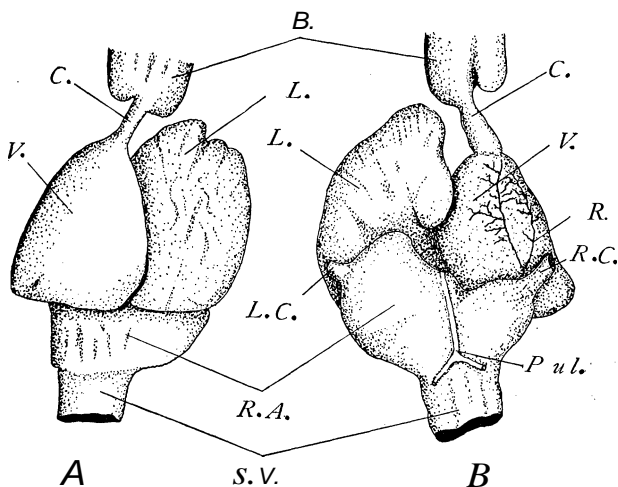


FIG. 14.—The heart. A, ventral. B, dorsal aspect. B., bulbus arteriosus; C., conus arteriosus; L., left auricle; L. C., left anterior vena cava; Pul., pulmonary; R., coronary vessels; R. C., right anterior vena cava; S. V., sinus venosus; V., ventricle.

leading from the anterior angle of the ventricle, and becoming enlarged at its anterior end to form the bulbus arteriosus that has just been described. It is unusually long, and its cylindrical shape and tough walls make it an excellent place into which to insert a cannula for the purpose of injecting the arterial system.

The ventricle (V.) is a thick-walled structure of a markedly triangular form, especially when seen from the ventral side (Fig. 14, A), with the apex of the triangle towards the head, where it opens into the truncus arteriosus. Owing to the thick muscular walls the ventricle remains smooth and of about the same size and shape

whether it be empty or distended. It forms the right anterior quarter of the heart, and lies somewhat ventral to the other parts of that organ.

The left auricle or atrium (*L.*) forms the left anterior quarter of the heart, and is its largest division, though on account of its thin distensible walls this chamber may vary considerably in size. Its walls are usually wrinkled and uneven, and its outline is more rounded than that of the ventricle, though the entire outline cannot be seen in either a dorsal or a ventral view, since the chamber is partially covered dorsally by the left auricle, and ventrally by the ventricle. At some point on its dorsal side the vein (*Pul.*) formed by the union of the two pulmonary veins probably enters it, but, on account of the very small size of this single pulmonary vein, its exact point of entrance could not be determined with certainty, and so has not been indicated in the figure. The size of the pulmonary veins in the figure has been exaggerated. The anterior edge of the left auricle lies nearer the head than any other part of the heart except the bulbus arteriosus.

The right auricle (*R. A.*) lies dorsal and posterior to the ventricle and the left auricle, so that in a ventral view of the heart only the posterior half of this chamber shows. Owing to its very thin walls and to the large opening of the sinus venosus it has no very definite shape. It is depressed in a dorso-ventral direction, and its greatest diameter is from side to side. Into its antero-lateral corners open the right and left anterior vena cava (*R. C.*, *L. C.*), while posteriorly it is separated by only a slight constriction, externally, from the sinus venosus which in turn is continued back as the posterior vena cava. Extending longitudinally across the dorsal wall of the right auricle, and closely attached to it, is the pulmonary vein (*Pul.*), formed by the union of the two small veins from the lungs.

The sinus venosus (*S. V.*) is merely the enlarged anterior end of the posterior or inferior vena cava. Its walls are extremely thin, and its size and shape will depend upon the amount of fluid it contains. Blood vessels to supply the walls of the heart may be seen at several places, and are shown in the figure at *R.*

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(No. 471 was issued March 22, 1906.)