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ANATOMY OF THE HEART OF THE AMPHIBIA II. *CRYPTOBRANCHUS ALLEGANIENSIS*

J. L. PUTNAM AND J. B. PARKERSON, JR.

ABSTRACT: This study of the heart of *Cryptobranchus alleganiensis* includes the first photographs of the organ. Among the new findings is a rudimentary septum in the sinus venosus and ventricle. Additionally, the interatrial septum, considered to be incomplete (perforated) previously, is found to have an extensive complete (non-perforated) component serving as a sinoatrial valve.

In conjunction with this anatomical work, we consider the comparative anatomy of the urodelan heart. Differences in position and shape of chambers suggest two phylogenetic histories for the urodelan heart, one encompassing the Sirenidae-Proteidae and the other encompassing all remaining urodeles including *Cryptobranchus alleganiensis*.

Key words: Anatomy; Heart; Urodela; *Cryptobranchus alleganiensis*

THE heart of *Cryptobranchus alleganiensis* is known from the early works of Branch (1935) and Reese (1906) who examined this organ in conjunction with a broader analysis of all bodily systems. Jollie (1962) included in his textbook a ventral view of all heart chambers except the sinus venosus but provided little discussion of heart structure. Noble (1925) studied the modifications within the atria and conus arteriosus resulting from the development of cutaneous respiration. Baker (1949) reviewed existing knowledge of the heart in conjunction with an analysis of aortic arches and their relationship to respiration and degree of metamorphosis. No study, devoted exclusively to the anatomy of the heart, appears in the literature.

MATERIALS AND METHODS

The hearts of 12 specimens of *Cryptobranchus alleganiensis* (purchased from Turtox/Cambosco and Sullivan Biological Supply) were studied. One of the 12 was observed in vivo with the animal under ether anesthesia. Anatomical relationships were noted in situ and with further dissection. Photographs were taken with an Olympus camera adapted to a Wild stereoscopic microscope.

RESULTS AND DISCUSSION OF COMPARATIVE ANATOMY

General Morphology

The heart of *Cryptobranchus alleganiensis* (Fig. 1A,B) is anterodorsal to the

coracoid cartilage of the pectoral girdle and lies within the parietal pericardium. Anteriorly, it is attached to the pericardial wall at the transition between the eight aortic arches and the truncus arteriosus and posteriorly (1) at the junction of the posterior vena cava and sinus venosus, (2) to the right and left ducts of Cuvier and to the right and left pulmonary veins where they pass through the parietal pericardium, and (3) along a line extending from the right and left ducts of Cuvier to the posterior vena cava. A cardiac ligament attaches the right dorsal wall of the ventricle to the anteroventral wall of the right duct of Cuvier. All attachment points stabilize the positions of the heart chambers regardless of pumping action.

Overall, the heart of *Cryptobranchus alleganiensis* lacks bilateral symmetry. The sinus venosus is located in the left posterior region of the pericardial cavity, a position that requires the right duct of Cuvier to be longer than the left. The atria are anterior to the sinus venosus and left anterolateral to the ventricle and have a clockwise rotation relative to the longitudinal body axis; this rotation places the right atrium anterior to the left. The ventricle is to the right of previously described heart chambers. The slightly twisted conus arteriosus, connecting to the right base of the ventricle, extends left anterolaterally to attach to the medial truncus arteriosus. Most urodeles (Bruner, 1900; Francis, 1934; Hopkins, 1896; Jo-

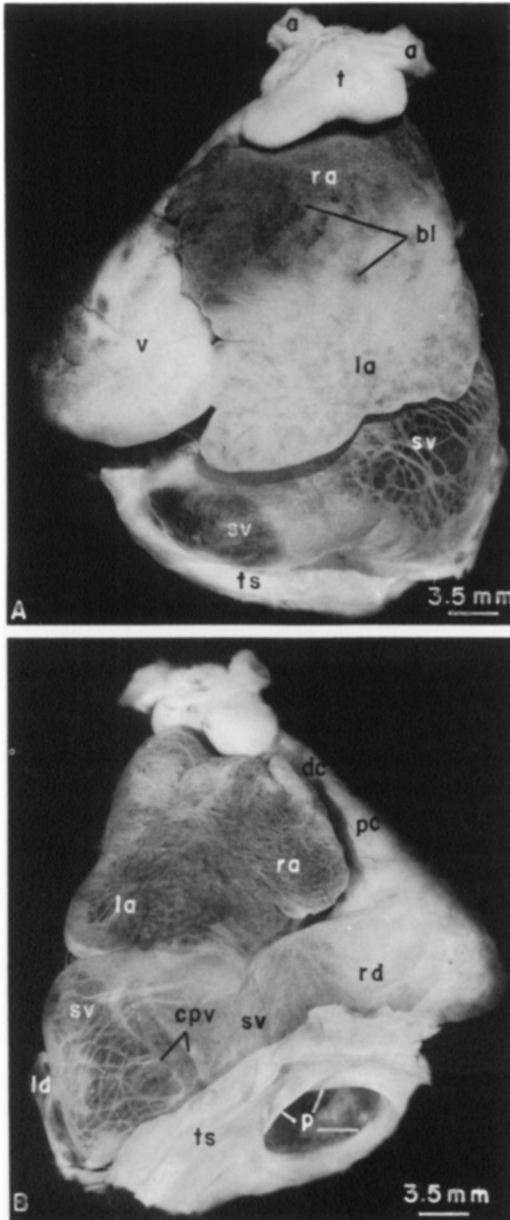


FIG. 1.—(A) Ventral view of the heart and associated vessels of *Cryptobranchus alleganiensis* in anatomical position. (B) Dorsal view of structures in Fig. 1A. *a* = aortic arches, *bl* = blood, *cpv* = common pulmonary vein, *dc* = distal conus arteriosus, *la* = left atrium, *ld* = left duct of Cuvier, *p* = aperture of posterior vena cava, *pc* = proximal conus arteriosus, *ra* = right atrium, *rd* = right duct of Cuvier, *sv* = sinus venosus, *t* = truncus arteriosus, *ts* = transverse septum, *v* = ventricle.

hansen, 1963) have similarly oriented heart chambers; only the Proteidae (Huxley, 1874) and Sirenidae (Putnam, 1977) differ significantly, with the heart chambers being more nearly bilaterally symmetrical.

Sinus Venosus

From the ventral view, the sinus venosus of *Cryptobranchus alleganiensis* is partially covered by the left atrium (Fig. 1A,B). This chamber has an expanded region to the left and a tapered conical region to the right. Reese (1906) considered the sinus venosus to be the right atrium.

The posterior vena cava enters the conical region of the sinus venosus through a distinct aperture formed by the connective tissue of the transverse septum (Figs. 1B, 2A,D). This oval aperture is oblique to the transverse plane. The right duct of Cuvier, after crossing half of the pericardial cavity, also enters the conical region just to the right of the postcaval aperture. The left duct of Cuvier opens into the expanded region of the sinus immediately after entering the pericardial cavity. Most urodeles have a similar arrangement of these three vessels, but in *Necturus maculosus* and *Siren lacertina*, the right and left ducts of Cuvier are equal in length, a reflection of the bilateral symmetry of the sinus venosus. *N. maculosus* uniquely possess right and left hepatic sinuses which connect the three incoming vessels to the sinus venosus.

The common pulmonary vein of *Cryptobranchus alleganiensis* (Figs. 1B, 2B,D) attaches to the dorsal wall of the sinus venosus and lies to the left of the mid-sagittal plane. Anteriorly, this vessel empties blood into the left atrium and posteriorly receives blood from the left and right pulmonary veins. The left pulmonary vein passes directly through the transverse septum to connect with the common pulmonary vein. The right pulmonary vein takes a more indirect route. After entering the transverse septum, it then extends left laterally, remaining within this septum and passing dorsal to

the aperture of the posterior vena cava. Finally, it emerges from the septum to connect with the common pulmonary vein. Branch (1935) described only right and left pulmonary veins in *C. alleganiensis* and indicated that they open into a posterior extension of the sinus venosus, the hepatic sinus. No hepatic sinus was observed in our study, and no pulmonary veins opened into the sinus venosus. All urodeles except lungless species (Bruner, 1900; Noble, 1931) have pulmonary veins, but the comparative anatomy of these vessels has not been studied.

The wall of the sinus venosus of *Cryptobranchus alleganiensis* is membranous with muscular trabeculae and connective tissue interspersed. Anastomosing bundles of muscle are better developed in the expanded region of the sinus (Figs. 1B, 2C), while connective tissue, appearing opaque in Fig. 1B, dominates in the conical. Both regions contract during the cardiac cycle, but the expanded one contracts more strongly and continues to contract after the conical region stops.

Internally, an incomplete dorsoventral sinal septum is present at the posterior end of the sinus venosus in 11 specimens of *Cryptobranchus alleganiensis* (Fig. 2A,D); one specimen had an undivided sinus venosus. This previously unreported septum is attached near the right lip of the aperture of the posterior vena cava and extends left anterolaterally, associating dorsally with the right pulmonary vein and the posterior region of the common pulmonary vein. In addition to the sinal septum, a single thread of trabecula attaches to the right and left lips of the aperture of the posterior vena cava in two specimens: in one of the two, a large columnar trabecula, which is about 1 mm anterior to the sinal septum, is also seen (Fig. 2D). The columnar trabecula is likely an anterior continuation of the sinal septum, because both have similar orientation and association with the common pulmonary vein. The function of the sinal septum and associated trabeculae is unclear, but they may divert blood toward the expanded re-

gion of the sinus which leads to the right atrium.

We propose that the sinal septum of *Cryptobranchus alleganiensis* is homologous with the better developed longitudinal septum of *Siren lacertina* (Putnam, 1977). In both species, the septum originates near the aperture of the posterior vena cava and associates with pulmonary veins. Longitudinal septa have not been reported in the sinuses of other urodeles. However, *Necturus maculosus* has unique right and left hepatic sinuses which in earlier proteids may have been not separate cavities, but a single cavity separated by a sinal septum. These proteids would have resembled contemporary *S. lacertina*, a possibility made plausible by heart similarities between *N. maculosus* and *S. lacertina*.

The sinoatrial aperture of *Cryptobranchus alleganiensis* opens anteriorly into the right atrium. This aperture is oblique to the transverse plane with the dorsal lip tilting anteriorly. Small papillae are seen along its margin and in one specimen, pocket valves are present ventrally (Fig. 2E). The common pulmonary vein, before opening into the left atrium, passes through the sinoatrial aperture at the dorsal lip. The sinoatrial aperture of urodeles is not described sufficiently well in the literature to provide a broad comparison with *C. alleganiensis*. However, Terhal's (1942) work on this aperture in *Salamandra salamandra* and *Ambystoma mexicanum* reveals a similar morphology.

Atria

The two atria of *Cryptobranchus alleganiensis* are completely visible dorsally, and ventrally the truncus arteriosus hides the anterior region of the right chamber (Fig. 1A,B). Externally, the two atria reveal no evidence of internal division. Reese (1906) called both atria the left atrium, and Branch (1935) considered them to be a single, undivided chamber.

The surface of the atria has undulations at the junction with the ventricle (Fig. 1A), and fimbriae occasionally are seen else-

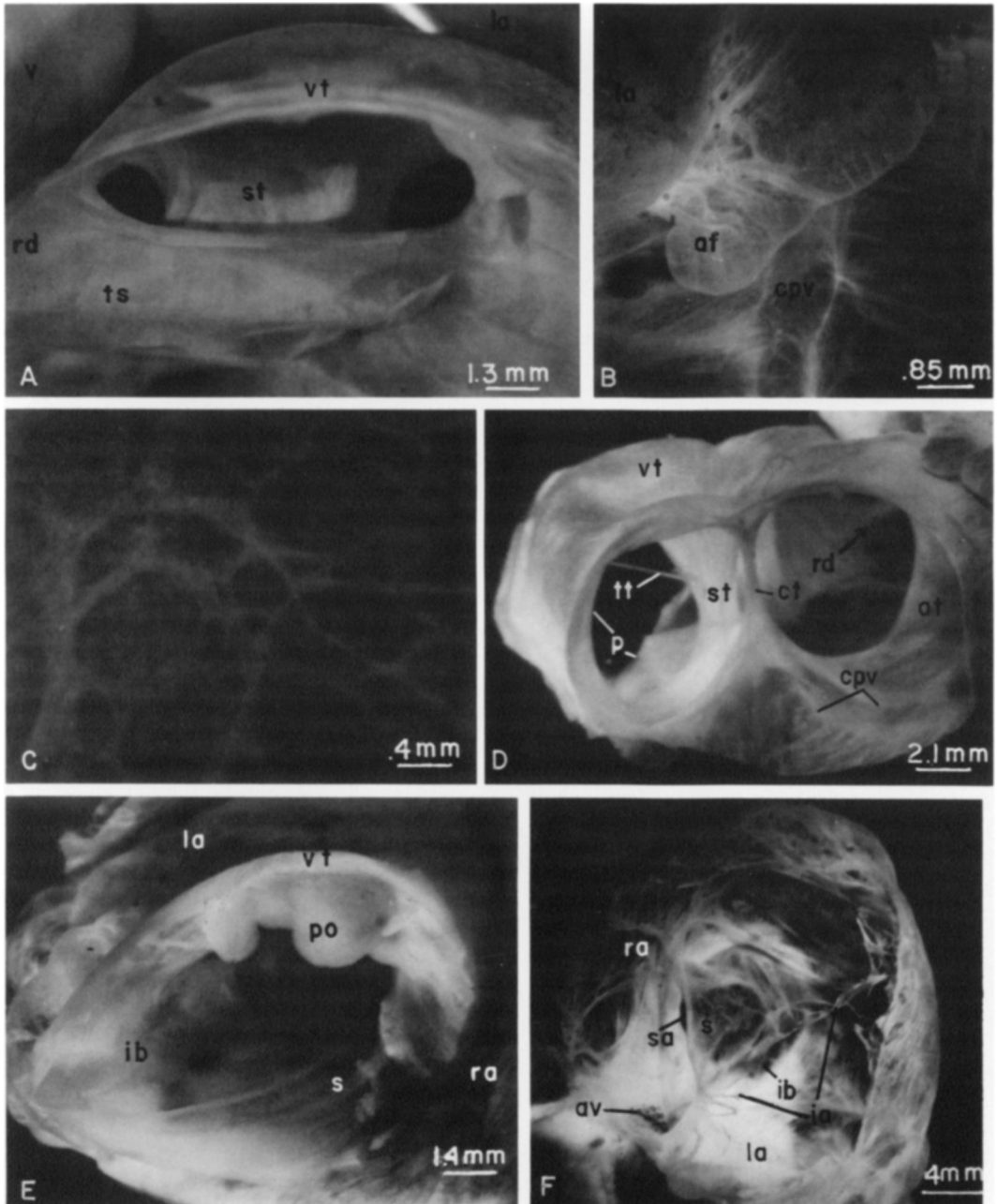


FIG. 2.—(A) Aperture of the posterior vena cava showing the septum within the sinus venosus. (B) Dorsal wall of the sinus venosus showing the common pulmonary vein and an atrial fimbria. (C) Muscular trabeculae of the dorsal wall of the sinus venosus. (D) Interior of the sinus venosus with most of the expanded region removed. The septum and other trabeculae are apparent. (E) Sinoatrial aperture showing the pocket valves, sinoatrial flap valve, and the non-perforated (complete) component of the interatrial septum. Photograph does not show the line separating the sinoatrial flap valve and the septum. (F) Section of both atria looking posteriorly toward the sinoatrial aperture. The two regions of the interatrial septum and the sinoatrial flap

where (Fig. 2B). A small auricle extends from the left atrium to cover the antero-ventral region of the sinus venosus. The walls of the atria are membranous as with the sinus venosus, but muscular trabeculae are better developed, some forming large ridges which protrude into the atrial lumina. Connective tissue is not readily apparent macroscopically.

The interatrial septum of *Cryptobranchus alleganiensis* lies in the transverse plane and divides the atrial cavity into larger right (anterior) and smaller left (posterior) chambers. This septum, described as incomplete in the literature (Baker, 1949; Jollie, 1962; Noble, 1925), has two distinct components, perforated (incomplete) and non-perforated (complete) (Figs. 2F, 3A,B).

The perforated component (*ia* in Fig. 3) of the septum attaches (1) near the ventral lip of the atrioventricular aperture, (2) to the ventral, left lateral and dorsal atrial walls, (3) to the non-perforated component (*ib* in Fig. 3) of the septum, and (4) to the sinoatrial flap valve (*s* in Fig. 3). This component, which is little more than anastomosing threads of trabeculae, provides for mixing of blood between the two atria. Other urodeles have incomplete atrial septation when they, like *Cryptobranchus alleganiensis*, depend on non-pulmonary respiration (Bentley and Shield, 1973; Czopek, 1965; Foxon, 1964; Guimond and Hutchison, 1972, 1976; Holmes, 1975; Johansen and Hanson, 1968; Lawson, 1979; Noble, 1925; Piiper et al., 1976; Simons, 1959). Lungless species were thought to have lost the interatrial septum completely (Bruner, 1900; Cords, 1924), but Putnam and Kelly (1978) described a remnant (*ia* in Fig. 3) of the structure in *Plethodon glutinosus*.

The non-perforated or complete com-

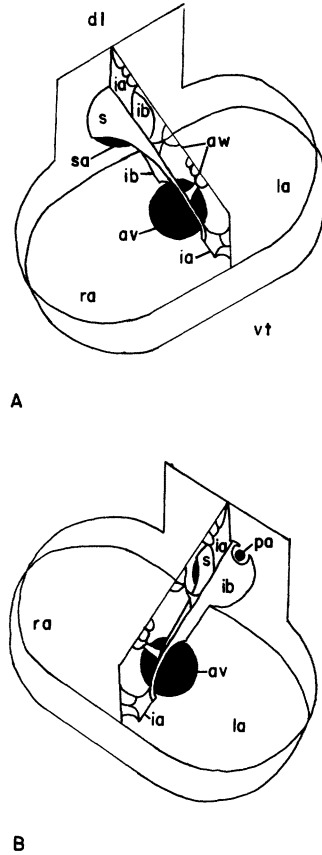


FIG. 3.—(A and B) Schematic view of the interior of the right and left atria showing the two components of the interatrial septum and the sinoatrial flap valve. *aw* = atrial wall where *ia* attached, *dl* = dorsal, *pa* = pulmonary aperture.

ponent (*ib* in Fig. 3) of the septum forms (1) an arch over the atrioventricular aperture, (2) attaches to the dorsal atrial wall, (3) partially circumscribes (about 180°) the sinoatrial aperture, (4) separates the sinoatrial and pulmonary apertures, and (5) connects with *ia* (in Fig. 3) and the sinoatrial flap valve (*s* in Fig. 3). This non-perforated component assists the sino-

valve are apparent. See Fig. 3 for schematic interpretation. *af* = atrial fimbria, *at* = anterior, *av* = atrioventricular aperture, *ct* = columnar trabecula, *ia* = perforated (incomplete) component of the interatrial septum, *ib* = non-perforated (complete) component of the interatrial septum, *po* = pocket valve, *s* = sinoatrial flap valve, *sa* = sinoatrial aperture, *st* = sinal septum, *tt* = thread of trabecula, *vt* = ventral.

atrial flap valve in closing the sinoatrial aperture. It is strategically positioned to facilitate this function, and in some fixed specimens, it and the sinoatrial flap valve were inserted into the sinoatrial aperture as if by back pressure generated when the atria contract. This proposed function for *ib* (in Fig. 3) explains (1) why the entire interatrial septum is not perforated or incomplete as might be expected in the non-pulmonic *Cryptobranchus alleganiensis* and (2) why the perforated and non-perforated regions are sharply delineated from one another where the sinoatrial flap valve attaches to them.

The sinoatrial flap valve (*s* in Fig. 3) attaches (1) at the junction of *ia* and *ib*, (2) to the dorsal and right lateral lips of the sinoatrial aperture (for about 90°), and (3) to the ventral lip of the atrioventricular aperture; it has a free margin extending into the right atrial cavity. Branch (1935) indicated that *Cryptobranchus alleganiensis* has a sinoatrial valve but was not clear as to whether it is a flap valve or a pocket valve. A sinoatrial flap valve has been described in all urodeles except for species of the Sirenoidea and Proteidae.

The atrioventricular aperture of *Cryptobranchus alleganiensis* lies parallel to the base of the ventricle. Large dorsal and ventral pocket valves and a smaller left lateral pocket valve guard this aperture (Figs. 4A, 5B). The three valves are supported by chordae tendinae which attach to the ventricular muscle. Jollie (1962) found four pocket valves of equal size guarding this aperture. All urodeles have at least two pocket valves except *Siren lacertina*, which has two plug-like valves. The dorsal and ventral valves are large and apparently the functional valves in *Salamandra salamandra* (Benninghoff, 1921; Boas, 1882; Bruner, 1900; Francis, 1934; Terhal, 1942), *Ambystoma mexicanum* (Boas, 1882; Terhal, 1942), lungless salamanders (Bruner, 1900) and *S. lacertina* (Putnam, 1977). The position of the two large valves is not reported in works on *Amphiuma tridactylum* (Johansen, 1963), *Notophthalmus viridescens*

(Hopkins, 1896), *Andrias japonicus* (Beddard, 1903) and surprisingly *Necturus maculosus* (Huxley, 1874; Walker, 1975; Wischnitzer, 1979). Small lateral valves or endocardial ridges, which have little or no valvular function, have been described in *S. salamandra* (Benninghoff, 1921; Terhal, 1942) and *A. mexicanum* (Terhal, 1942).

Ventricle

The triangular ventricle of *Cryptobranchus alleganiensis* (Fig. 1A,B) has an apex directed right posteriorly and a base lying oblique to the transverse plane. A broad cardiac ligament connects two-thirds of its right dorsal wall to the anteroventral wall of the right duct of Cuvier (Fig. 4B); in one specimen, the ligament extends fully along the right dorsal wall (i.e., from the right base to the apex). A right lateral coronary vein is found along the surface of the ventricle and originates from dorsal and ventral vessels on the conus arteriosus and terminates at the right duct of Cuvier only after coursing through the posterior region of the cardiac ligament; smaller coronary veins from the dorsal and ventral surfaces of the ventricle open into the right lateral coronary vein. Two or more small coronary veins empty directly into the right duct of Cuvier after passing through the cardiac ligament. In two specimens, a right dorsal coronary vein is found about 5 mm from the right lateral vessel; both vessels are the same size and become confluent as they enter the cardiac ligament.

Cardiac ligaments and coronary vessels are too poorly known to draw conclusions about their comparative anatomy; Terhal (1942) provided the best discussion of these structures.

The wall of the ventricle of *Cryptobranchus alleganiensis* is formed by muscular trabeculae as in other urodeles. These trabeculae anastomose with one another, vary in diameter and length, and form a generally circular pattern (Fig. 4C,D,E). Blood is found among the trabeculae to near the surface of the ventricle. A large

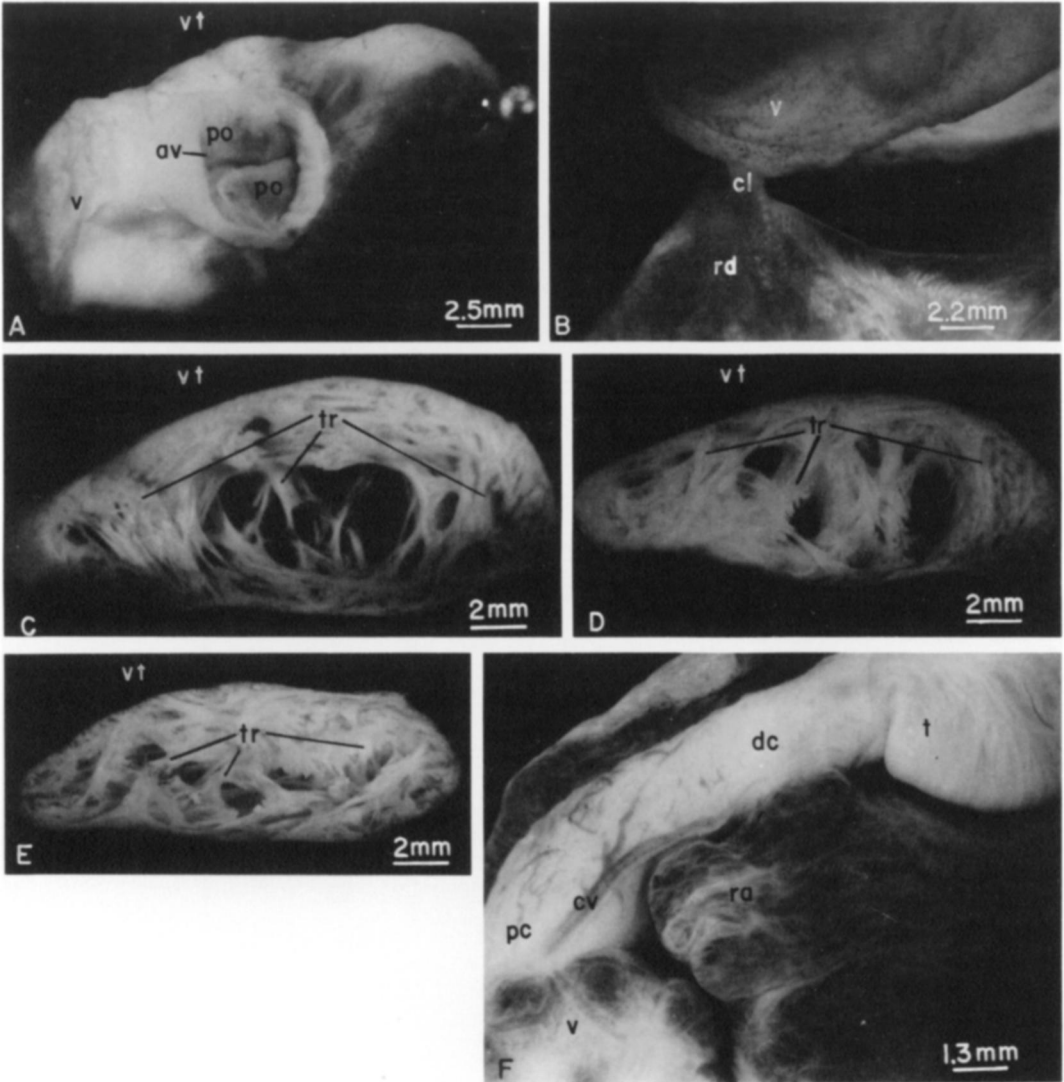


FIG. 4.—(A) Cross section through the atrioventricular aperture showing dorsal and ventral pocket valves. The left lateral valve is not visible. (B) Cardiac ligament connecting ventricle to the right duct of Cuvier. (C) Cross section of the ventricle immediately posterior to the unitary cavity of the ventricle. (D) Cross section 3 mm posterior to C. (E) Cross section 3 mm posterior to D. (F) Ventral view of the heart showing the left ventral coronary vein on the conus arteriosus. *cl* = cardiac ligament, *cv* = coronary vein, *tr* = trabeculae.

cavity is immediately posterior to the atrioventricular and conal apertures and is interrupted posteriorly by muscular trabeculae which course primarily dorsoventrally. These trabeculae create numerous pockets, the largest lying within the cen-

tral region of the ventricle (Fig. 4C,D). Trabeculae in the left side of the ventricle (Fig. 4C) resemble in two ways those which constitute the interventricular septum of *Siren lacertina* (Putnam, 1977) and *Necturus maculosus* (Putnam and Dunn,

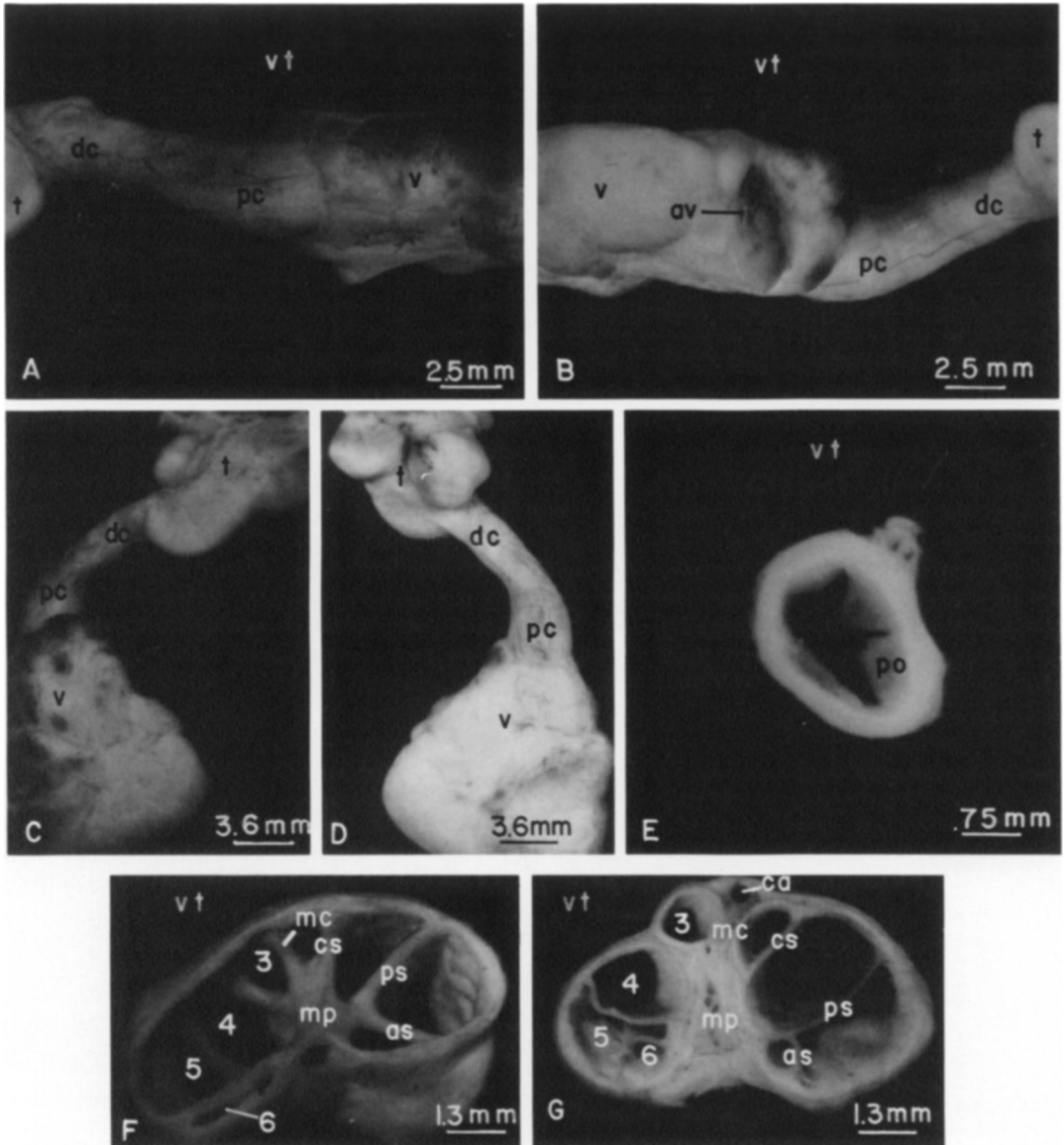


FIG. 5.—(A) Right lateral view of the heart showing ventral bend in the conus arteriosus. (B) Left lateral view of the structures in A. (C) Ventral view of the heart chambers with atria and sinus venosus removed. (D) Dorsal view of the structures in C. (E) Cross section of conus arteriosus showing pocket valves. (F) Cross section of the truncus arteriosus at the origin of the four pairs of aortic arches. (G) Cross section of the truncus arteriosus just before the aortic arches separate from the truncus. *as* = accessory septum, *ca* = coronary artery, *cs* = caroticoaortic septum, *mc* = medial carotid septum, *mp* = medial pulmonic septum, *ps* = principal septum.

1978). They (1) form a large aggregate of muscle (i.e., as wide as the ventricular walls) and (2) extend dorsoventrally and anteroposteriorly. However, these trabeculae fail to align with the atrioventricular aperture as they do in *S. lacertina* and *N. maculosus*. Thus, the trabeculae should not be considered an interventricular septum, but a possible remnant structure. An interventricular septum has not been reported in any other urodeles although vestigial septation has been described in apodans (Lawson, 1966; Marcus, 1935; Ramaswani, 1944; Schillings, 1935) and *Triturus helveticus* (Turner, 1966).

The aperture of the conus arteriosus is at the right base of the ventricle (Figs. 4F, 5C,D). This opening, unlike the atrioventricular, is oblique to the ventricular base. All urodeles have the conal aperture at the right base.

Conus Arteriosus

The proximal region of the conus arteriosus of *Cryptobranchus alleganiensis* extends anteriorly from the right base of the ventricle (Fig. 4C,D). A slight, somewhat distal bend, marks the transition to the distal region and redirects the conus left anteroventrally (Fig. 5A,B). A second bend, occurring at the transition between the distal region of the conus and truncus arteriosus, is somewhat obscured by the bulbous morphology of the truncus. The conus arteriosus of all urodeles has two bends.

The venous system is well developed over the surface of the conus arteriosus of *Cryptobranchus alleganiensis* (Fig. 4F). Left ventral and left dorsal coronary veins connect to the right lateral coronary vein of the ventricle. The left dorsal coronary vein also opens into the right dorsal coronary vein of the ventricle when the latter is present. A coronary artery, originating on the truncus arteriosus, is on the ventral surface of the distal region of the conus arteriosus but becomes obscure in the musculature before reaching the proximal region.

The wall of the conus arteriosus of *Cryptobranchus alleganiensis* is composed of compact muscular tissue (Fig. 5E), a contrast to the trabecular muscle of all previously described chambers. A single row of five pocket valves, positioned about 3 mm from the ventricle, is present in the proximal region of the conus. The left valve is the largest, the ventral one is the smallest, and the two dorsal and one right lateral valves are intermediate in size. Jollie (1962) reported four pocket valves of equal size in the proximal region. The distal region of the conus has a single row of four pocket valves about 2 mm from the truncus arteriosus; Jollie reported five. These valves are all the same size, and the pocket depth is twice that of the large left valve in the proximal region. This size differential argues for greater importance of the distal pocket valves in preventing blood backflow. The proximal and distal rows of pocket valves are 2 mm apart, a distance much closer than indicated by Jollie (1962). No spiral valve is present.

Three proximal pocket valves have been observed in all urodeles except *Cryptobranchus alleganiensis* and *Siren lacertina* (Putnam, 1977) which have four. Intraspecific variation has been observed in *Ambystoma mexicanum* and *Salamandra salamandra* (Terhal, 1942) where a fourth valve, usually rudimentary, has been noted. Four distal pocket valves have been reported in most urodeles. *Plethodon glutinosus* (Noble, 1925) and *Necturus maculosus* (Huxley, 1874) are exceptions with three valves. The spiral valve, not found in *C. alleganiensis*, is also absent in *N. maculosus*. Lungless salamanders according to Noble (1925) do not have a spiral valve, but Putnam and Kelly (1978) reported one in *P. glutinosus*, albeit rudimentary. A spiral valve has been observed in *S. salamandra* (Francis, 1934; Terhal, 1942), *A. mexicanum* (Terhal, 1942), *Amphiuma tridactylum* (Johansen, 1963) and *S. lacertina* (Putnam, 1977). Non-pulmonic respiration in urodeles is correlated with the reduction of or loss of the spiral

valve (Bentley and Shield, 1973; Czopek, 1965; Foxon, 1964; Guimond and Hutchison, 1972, 1976; Holmes, 1975; Johansen and Hanson, 1968; Lawson, 1979; Noble, 1925; Piiper et al., 1976; Simons, 1959).

Truncus Arteriosus

The truncus arteriosus of *Cryptobranchus alleganiensis* (called bulbous arteriosus by Branch, 1935; Reese, 1906) is anterior to the conus, is bulbous (Fig. 5C,D) and has four pairs of aortic arches extending from its right and left anterior edges (Fig. 1A,B). A bulbous truncus occurs in other urodeles except *Siren lacertina* and *Necturus maculosus* which have the truncus elongate.

The coronary veins of *Cryptobranchus alleganiensis* form a network of vessels on the surface of the truncus arteriosus, but no major vessels are apparent. A coronary artery lies near the mid-ventral line and continues onto the conus arteriosus.

The wall of the truncus arteriosus of *Cryptobranchus alleganiensis* is composed of compact, non-trabecular tissue as in the conus. Several septa originate in the truncus at its junction with the conus (Fig. 5F,G) and extend anteriorly to form aortic channels; these channels emerge from the truncus as aortic arches. Medial carotid and pulmonic septa together divide the truncal cavity into right and left halves. Two caroticoaortic septa extend from the medial carotid septum to the right and left ventral wall of the truncus forming parts of the third and fourth pairs of aortic channels. The two principal septa extend from the medial pulmonic septum to the right and left ventrolateral wall. These septa form parts of the fourth and fifth pairs of aortic channels. Two accessory septa extend from the principal septa and/or the medial pulmonic septum to connect with the right and left dorsolateral wall of the truncus, thus contributing to the formation of the fifth and sixth aortic channels.

Branch (1935) found two, three and four pairs of aortic arches extending from the truncus of *Cryptobranchus alleganiensis*.

In those specimens with fewer than four pairs, the truncal septa are presumably reduced although Branch does not report this. No variation in numbers of aortic channels or arches was observed in our study.

In urodeles, the number of pairs of aortic arches leaving the truncus arteriosus varies from two to four. Those urodeles with four pairs include, in addition to *Cryptobranchus alleganiensis*, *Salamandra salamandra* (Boas, 1882; Francis, 1934), *Ambystoma maculatum* (Noble, 1925), *Amphiuma tridactylum* (Putnam and Sebastian, 1977) and *Andrias japonicus* (Beddard, 1903). Variation is found among some of these species and closely related ones. For example, *S. salamandra* (Terhal, 1942) may have only the right or left fifth arch, and one arch or the other may never emerge from its aortic channel, thus ending as a blind pouch. *Ambystoma mexicanum* (Terhal, 1942) always has four pairs of aortic arches, but the pulmonary arch in some species branches from the fifth aortic channel at the anterior end of the truncus; thus only three pairs of channels are seen throughout most of the length of the truncus. *A. tridactylum*, which has four pairs of arches according to Putnam and Sebastian (1977), is reported by Johansen (1963) and Baker (1949) to have three, the fifth being absent. Three pairs, third, fourth and sixth, are reported in *Ambystoma opacum* (Noble, 1925).

Many plethodontid salamanders have three pairs of aortic arches arising from the truncus, but it is not clear whether the fifth or sixth pair is eliminated. McMullen (1938), studying *Desmognathus fuscus* and *Plethodon cinereus*, noted the presence of the fifth pair, while Bruner (1900), Cords (1924) and Noble (1925) reported this arch to be the sixth. *Siren lacertina* also has three pairs of aortic arches arising from the truncus, but unlike plethodontids, the dorsal pair gives rise to the fifth and sixth arches after leaving the truncus. *Necturus maculosus* (Baker, 1949) and *Eurycea bislineata* (McMullen, 1938) have

only two pairs of aortic arches arising from the truncus. In *N. maculosus*, one pair gives rise to the third arch, while the other pair bifurcates after leaving the truncus to give rise to the fourth and fifth pairs. *E. bislineata* has only the third and fourth arches in the adult although the fifth is present in the larva.

Variation in numbers of aortic arches and channels is reported in each suborder of urodeles. While causality has not been determined in every case, variations seem largely attributable to reduction in or loss of pulmonic respiration.

When the truncus arteriosus is elongate as in *Siren lacertina* (Boas, 1882; Putnam, 1977) and *Necturus maculosus* (Baker, 1949), a sagittal septum posterior to the aortic channels divides the structure into right and left halves; this septum is about half the total length of the truncus and fuses anteriorly with the medial carotid and pulmonic septa.

In summary, our comparative study of the heart of urodeles reveals considerable variation. Variability in position and shape of heart chambers suggests two phylogenetic histories for the urodelan heart, one including the Sirenidae-Proteidae and the other including all remaining urodeles.

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THE MICROSTRUCTURE AND EVOLUTION OF SCALE SURFACES IN XANTUSIID LIZARDS

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ABSTRACT: The microstructure of the dorsal scales in 12 of the 16 species of xantusiid lizards is examined by scanning electron microscopy and compared with that of species reported elsewhere and five species described for the first time here (*Gerrhosaurus nigrolineatus*, *Anadia bogotensis*, *Echinosaura horrida*, *Pachydactylus bibronii* and *Hemidactylus brookii*).

Cricosaura typica and all three species of *Xantusia* have a lamellate cell arrangement. Lamellae and cells with a large, dome-like central projection (micro-dome morphotype) are present in all *Lepidophyma* examined. Five species of *Lepidophyma* also have cells with a large, tubercle-like projection (micro-tubercle morphotype). The addition of micro-tubercles to the range of morphotypes is associated with the presence of keeled tubercular scales. Structures which superficially resemble the micro-tubercles occur in several non-xantusiid species which also have tubercular scales, but their shape and construction suggest that they are not homologous with those of xantusiids. The micro-dome and micro-tubercle morphotypes appear to be unique to xantusiids. The lamellate cell arrangements of xantusiids are similar to those of a variety of anguimorph and scincomorph species. Comparative data supplemented by a morphotypic series based on topographic gradients between morphotypes suggest that (1) the micro-dome morphotype is derived from lamellate cells, and (2) the morphotypic series (micro-dome to micro-ridge to micro-tubercle) replicates the evolutionary sequence in derivation of the morphotypes.

The lamellate cell arrangement is judged to be primitive within the Lacertilia and is found in all members of the Xantusiidae. Spinules and juxtaposed cell boundaries, derived features found in gekkonids, are absent in xantusiids. Uniquely derived characters include: a particular type of dorsal scale organ for the Xantusiidae, cells bearing a micro-dome for *Lepidophyma*, and cells bearing a micro-tubercle for five species of *Lepidophyma*.

Key words: Reptilia; Sauria; Xantusiidae; Scale microstructure; Scale evolution

RECENT studies suggest that the microstructure of scale surfaces in lizards and snakes (1) is characterized by striking morphological innovations and patterns of