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El desarrollo de las venas en el gato doméstico (*Felis domestica*), con especial mención de: 1) la participación de las venas supracardinales en el desarrollo de la postcava y vena azigos, y 2) la interpretación de las condiciones de variación de la postcava y sus tributarios encontradas en el adulto.

Esta investigación fué comenzada en 1905 con el propósito de determinar el plan venoso ontogénico normal que serviría como base para explicar las variaciones observadas en el gato adulto como resultado de un desarrollo atípico de las venas. El trabajo vá ilustrado con doce figuras en colores, basadas en reconstrucciones en cera, y dichas figuras servirán también para explicar las condiciones observadas por los autores en el hombre. Algunos de los puntos mas importantes tratados por los autores son los siguientes: 1. La división postrenal de la vena postcava se deriva exclusivamente de una parte de las venas subcardinales, partir endo del lado derecho de lo que los autores han llamado el cuello renal, y de las venas supracardinales. Ninguna parte se deriva principalmente de las venas postcardinales. 2. Las venas azigos se derivan de las supracardinales. 3. Una nueva interpretación sobre el desarrollo de las venas sexuales. 4. Un esquema compuesto que presenta combinados todos los trayectos venosos que pueden aparecer durante la ontogenia. Por medio de este esquema se pueden interpretar los diecisiete tipos en los cuales pueden clasificarse las variaciones de la postcava encontradas en el gato y en el hombre.

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THE DEVELOPMENT OF THE VEINS IN THE DOMESTIC CAT (*FELIS DOMESTICA*) WITH ESPECIAL REFERENCE, 1) TO THE SHARE TAKEN BY THE SUPRA-CARDINAL VEINS IN THE DEVELOPMENT OF THE POSTCAVA AND AZYGOS VEINS AND 2) TO THE INTERPRETATION OF THE VARIANT CONDITIONS OF THE POSTCAVA AND ITS TRIBUTARIES, AS FOUND IN THE ADULT

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TWELVE FIGURES (IN COLORS)

This investigation was begun in 1905. In the preceding years we had found that the variations or atypical conditions of the venous system observed by Darrach,¹ McClure² and others in the adult cat could not all be explained on the basis of the existing knowledge of the development of the veins. We therefore determined to study in detail the normal ontogenetic plan of the veins in the cat, with the hope that we might be able to interpret correctly the variant conditions of the venous system which arose as the result of atypical development of the veins.³

We have recently extended our observations to a study of the development of the veins in man, the pig and the rat, and while

¹ Darrach, W. 1907. Variations in the postcava and its tributaries as observed in 605 examples of the domestic cat. *Proc. Amer. Ass. Anat., Amer. Jour. Anat.*, Vol. 6.

² McClure, C. F. W. 1900. On the frequency of abnormalities in connection with the postcaval vein and its tributaries in the domestic cat (*Felis domestica*). *Amer. Nat.*, Vol. 34.

³ Huntington, G. S., and McClure, C. F. W. 1907. The Development of the Postcava and Tributaries in the Domestic Cat. *Proc. Amer. Ass. Anat., Amer. Jour. Anat.*, Vol. 6.

it has been observed that important generic differences exist in the pig and the rat, the development of the veins in man has been found to resemble more closely that observed in the cat.⁴

Although our investigation has been completed, it may be some time before the detailed publication is ready for the press. We have therefore deemed it advisable to publish a preliminary summary of our work in the form of a series of diagrams which illustrate the normal ontogenetic plan followed by the veins, with especial reference, however, to the share taken by the supracardinal system of veins in the development of the azygos vein and of the postrenal division of the postcava in the cat. A brief summary is also given of the potential postcaval variants in the adult cat and man. An explanation of these variant conditions is based on a composite diagram (fig. 12) combining all of the venous pathways which may arise during ontogeny and which are potentially capable of being retained in the adult in atypical individuals.

The diagrams which we present are based on a large series of wax reconstructions made after the method of Born, of cat embryos ranging between 5 and 45 millimeters in length. They represent a series of critical ontogenetic stages leading from the early primitive venous groundplan common to all vertebrates (fig. 1), up to the conditions obtaining in the adult cat.

In constructing these diagrams it was deemed desirable to include all of the main axial venous channels of the body other than those investigated by us, and we fully appreciate and acknowledge that the previous contributions of other investigators, especially those of Rathke,⁵ Hochstetter⁶ and F. T. Lewis,⁷ have made this possible.

⁴ Huntington, G. S. and McClure, C. F. W. 1920. A series of diagrams explanatory of the development of the postcava in the cat, with especial reference to the share taken by the supracardinal system of veins. *Proc. Amer. Ass. Anat., Anat. Rec.*, Vol. 18.

⁵ Rathke, H. 1838. Ueber den Bau und Entwicklung des Venensystems der Wirbeltiere. Dritte Bericht über das Naturwissenschaftliche Seminar zu Königsberg. Idem. 1832. Abhandlungen zur Bildungs- und Entwicklungsgeschichte des Menschen und der Thiere. Leipzig, T. I.

⁶ Hochstetter, F. 1893. Beiträge zur Entwicklungsgeschichte des Amnioten, III, Säuger, *Morph. Jahrb.*, Bd. 20.

⁷ Lewis, F. T. 1902. The development of the vena cava inferior. *Amer. Jour. Anat.*, Vol. 1.

The uniform color scheme shown in the figures makes it easy to follow the transformations of the embryonic venous system through the different stages of its development. Only a brief account of each critical stage will be given in the present paper, while a more detailed description will be reserved for a later publication in which the actual reconstructions will be demonstrated on which our observations have been based.

FIG. 1. CARDINO-SUBCARDINAL STAGE.

This stage of development may be regarded as representing a common groundplan of the vertebrate embryonic venous system. It forms the starting point which is succeeded by a series of modifications gradually leading up to the conditions observed in the adult. In some cases these modifications are brought about by the persistence or atrophy of certain of its component vessels, while in others, modifications arise by the addition of newly-formed vessels to the primary groundplan. The diagrams we present illustrate these modifications of the embryonic groundplan as observed in the embryo of the cat.

The principal vessels of the embryonic venous groundplan consist of three pairs of essentially bilateral symmetrical veins, viz.: the precardinal (*Prc.*) and postcardinal (*Pc.*) veins which open in common into the sinus venosus through the ducts of Cuvier (*D.C.*) and the subcardinal (*Subc.*) veins. The postcardinal veins lie dorsal to the mesonephroi, while the subcardinals lie ventro-medial to the same. Anastomoses between the postcardinal and subcardinal veins are present and intersubcardinal anastomoses are met with caudal to the origin from the aorta of the omphalomesenteric artery.

The sex veins from the gonads (*G*) open into the subcardinal veins at this stage. The veins of the liver drain for the most part directly into the sinus venosus through the *V. hepatica communis* (*V.H.C.*) and no connection between the liver circulation and the right subcardinal vein has as yet been formed.

The blood collected from the body-walls and mesonephroi by the postcardinals, as well as that carried by the subcardinal veins, is returned to the heart through the ducts of Cuvier (*D.C.*) in common with that brought from the head region and anterior limb-buds by the precardinal veins.

FIG. 2. ESTABLISHMENT OF THE PARS HEPATICA AND PARS SUBCARDINALIS OF THE POSTCAVA, CONSTITUTING THE PRERENAL DIVISION OF THE POSTCAVA IN THE ADULT.

The significant features of this stage of development, are the establishment of the prerenal division of the adult postcava, and the beginning replacement of an originally bilaterally symmetrical by a subsequent asymmetrical plan of axial venous organization.

As shown by F. T. Lewis, the prerenal division of the postcava is formed by the establishment of a communication between the veins of the liver and the right subcardinal vein. The point at which this communication is established with the right subcardinal has been previously designated by one of the writers⁸ as the hepato-subcardinal junction (*Hep.Subc.Jct.*).

The portion of the prerenal division of the postcava which lies cranial to the hepato-subcardinal junction may be termed the *pars hepatica* (*P.Hep.*). It is formed *in situ* by a rearrangement and transformation of vascular channels already formed, viz., by the V. hepatica communis, the hepatic sinusoids and by the vascular area formed within the caval mesentery.

The portion of the prerenal division of the postcava which lies caudal to the hepato-subcardinal junction is known as the *pars subcardinalis* (*P.Subc.*), as it is formed largely by a portion of the right subcardinal vein. Slightly caudal to the origin of the omphalomesenteric artery from the aorta, the pars subcardinalis establishes a wide communication with the left subcardinal, through an intersubcardinal anastomosis (*Int.Subc.Anast.*) and also one with each postcardinal, by the enlargement of one of the anastomoses that exist at this level between the intersubcardinal anastomosis and the postcardinal veins (subcardino-postcardinal anastomoses, *Subc.Pc.Anast.* (fig. 12)).

As the result of these modifications of the early embryonic groundplan, the blood from the region of the body which lies caudal to the intersubcardinal anastomosis (body-walls and mesonephroi) is now, for the most part, directed from the postcardinal (*Pc.2*), on both sides of the body, through the subcardino-post-

⁸ McClure, C. F. W. 1906 A contribution to the anatomy and development of the venous system of *Didelphys marsupialis* (L.). Amer. Jour. Anat., Vol. 5, p. 171.

cardinal anastomosis to the prerenal division of the postcava. Also, correlated with these changes, the postcardinals (*Pc.2*), caudal to the intersubcardinal anastomosis, become greatly enlarged, while the segments cranial (*Pc. 1*) to this anastomosis become reduced and return blood from the body-walls of the thoracic region and from the cranial end of the mesonephroi directly to the heart by the ducts of Cuvier (*D.C.*).

The sex veins still open into the subcardinal veins. Anastomoses are also still present between the subcardinal and postcardinal veins, caudal to the intersubcardinal anastomosis, which form part of the mesonephroic circulation. In the region cranial to the intersubcardinal anastomosis, however, the subcardinals soon become associated with the anlagen of the adrenal bodies forming the main venous drainage line of these organs which is retained throughout subsequent stages of development.

FIG. 3. FURTHER TRANSFORMATIONS OF THE POSTCARDINAL AND SUBCARDINAL VEINS WHICH ARE ASSOCIATED LARGELY WITH THE GROWTH OF THE MESONEPHROS.

SEPARATION OF THE POSTCARDINAL VEINS INTO A THORACIC AND LUMBAR DIVISION.

The originally continuous postcardinals have now become divided into a cranial or thoracic (*Pc.1*), and into a caudal or lumbar (*Pc.2*) pair of veins. The former collect the blood chiefly from the body-walls of the thorax and from the anterior portion of the mesonephroi, while the latter drain the more caudal regions of the body.

The lumbar division of the postcardinal (*Pc.2*), on each side of the body, now encircles the relatively large mesonephros, both dorsally and medially, so that in reconstructions of the veins at this stage each mesonephros appears to be arched over by or to lie within a great venous basket or trough formed by the postcardinal vein and its subcardinal anastomoses.

The permanent kidneys (*K*) have migrated cranial from their earlier position ventral to the umbilical arteries and now occupy a position dorsal to the lumbar postcardinals (*Pc.2*).

Cranial to the intersubcardinal anastomosis (*Int.Subc.Anast.*) the subcardinal veins, except that portion of the vein of the right

side which forms the pars subcardinalis of the postcava (*P.Subc.*), have become still more closely associated with the adrenal organs so that from now on, we may speak of these veins as the adrenal veins (*Adr.*). Caudal to the intersubcardinal anastomosis the subcardinal veins have lost their original continuity so that the sex veins, of subcardinal origin, now drain directly into the postcardinals (*Pc.2*), as well as into the intersubcardinal anastomosis. The significance of this observation lies in the circumstance that the sex veins at this time are exclusively of subcardinal origin, a condition which is retained in the adult of lower vertebrates, up to and including birds.

FIG. 4. THE ESTABLISHMENT OF THE SUPRACARDINAL SYSTEM OF VEINS AND THE RENAL COLLAR.

A bilateral and originally symmetrical venous channel develops dorso-medial to the primitive postcardinal and dorso-lateral to the aorta, into which the somatic postcardinal tributaries secondarily drain. This secondary venous channel forms what we have termed the *Supracardinal System of Veins* (*Sprc.*). It extends, from the level at which the posterior limb veins unite with the postcardinals, to a point cranial where it joins that portion of the postcardinals (*Pc.1*) which alone persists to form the cranial end of the adult azygos (*Az.*) veins. Between these levels the supracardinal veins come to enter into the definite organization of both the adult postcava in its postrenal division and of the azygos in its lumbar and part of its thoracic segments, entirely replacing in these districts the primitive postcardinal veins.

"It is important to note that the supracardinal veins are not in any sense merely synonyms for the dorsal limb of the periureteric ring described by Hochstetter and others, but comprise a continuous morphologically uniform system of longitudinal venous channels which contribute to the establishment of the adult condition in both the postcaval and azygos areas."⁹

The beginning of the establishment of the supracardinal system of veins takes place at a relatively early stage of development, and its cranial extension into the thoracic region is evidence that its appearance is not primarily associated with the cranial migration of the permanent kidneys. Frequent anastomoses occur

⁹ Loc. cit., footnote 3.

between the postcardinals and supracardinals at an early stage of development and, at this time, the anastomoses between the right and left supracardinal veins (intersupracardinal anastomoses), as shown in figure 4, have not yet been formed.

The early anastomoses between the supracardinal and postcardinal veins soon undergo atrophy and disappear. A large single anastomosis (fig. 4, *R.Col.*), at about the level of the intersubcardinal anastomosis, is retained, however, on each side of the body, which permits blood collected by the supracardinals in the lumbar region to reach the heart by way of the prerenal division of the postcava. This anastomosis we have designated as the subcardino-supracardinal anastomosis (*R.Col.*, fig. 4), since, in the later stages, it appears to connect the subcardino-postcardinal anastomosis with the supracardinal vein.

The blood collected by the supracardinal veins which is not directed to the prerenal segment of the postcava through the subcardino-supracardinal anastomosis, reaches the heart by way of the ducts of Cuvier (*D.C.*).

The formation of this subcardino-supracardinal anastomosis, at about the level of the intersubcardinal anastomosis, establishes the presence of a circum-aortic venous ring at this point which we have designated as the *Renal Collar*.

In order to appreciate the topographical relations of the renal collar to the main venous channels and the aorta, the reader is referred to fig. 12, a diagram based largely on the reconstruction of a 16 millimeter embryo of the cat. As clearly shown here, the renal collar is formed by the pars subcardinalis of the postcava (*P.Subc.*), the intersubcardinal anastomosis (*Int.Subc. Anast.*), the right and left subcardino-postcardinal anastomoses (*Subc.Pc.-Anast.*), the right and left subcardino-supracardinal anastomoses (*Subc.Sprc.Anast.*), the right and left supracardinals (*B* and *C*) and the anastomoses between the supracardinals dorsal to the aorta at this point, at which level the renal veins (*R.V.*) enter the collar.

The sex veins (fig. 4) still join the postcardinals and, in some cases, as shown in fig. 3, they may also open into the intersubcardinal anastomosis, a condition which is occasionally retained in the adult when multiple sex veins are present.

FIGURE 5. PROGRESSIVE DEVELOPMENT OF THE BILATERAL, SYMMETRICAL SYSTEM OF SUPRACARDINAL VEINS.

SEPARATION OF THE SUPRACARDINALS INTO AN AZYGOS AND LUMBAR DIVISION.

COMPLETION OF THE CRANIAL MIGRATION OF THE PERMANENT KIDNEYS, THE DEVELOPMENT OF THE RENAL VEINS AND THE ESTABLISHMENT OF THE PERIURETERIC VENOUS RINGS.

The supracardinal veins (*Sprc.*) at first undergo a progressive development during which their bilateral symmetry is retained for a considerable period of time. They soon separate, however, into a cranial or azygos and into a caudal or lumbar pair of veins, from which the azygos veins and a segment of the postrenal division of the adult postcava are, respectively, derived.

The bilateral symmetrical pair of supracardinals in the lumbar region anastomose freely with each other dorsal to the aorta and become greatly increased in size. Blood which they receive from the body-walls through four pairs of dorsal tributaries, and that received by them from the external (*E.II.*) and internal iliac (*I.II.*) veins, now reaches the prerenal segment of the postcava exclusively through the right and left subcardino-supracardinal anastomoses (lateral portion of renal collar, *R.Col.* fig. 5), which have become correspondingly enlarged.

Blood collected by the supracardinals in the thoracic region (azygos veins), chiefly from the body-walls, is returned to the heart through the right and left ducts of Cuvier (*D.C.*), in common with that collected from the head region and anterior limbs by the precardinal veins.

The permanent kidneys (*K*) have completed their migration craniad, and the hilus of each kidney now lies at about the level of the renal collar (fig. 12). After the migration of the kidneys has been completed, the permanent renal veins (*R.V.*) are formed. These consist at first of a right and left pair of renal veins which extend between the hilus of each kidney and the lateral portion of the renal collar (*R.V.*, fig. 12).

The relation of the renal veins to the lateral portion of the renal collar (subcardino-supracardinal anastomosis) is shown in figs. 8 and 9 which are lateral views of the right side of actual recon-

structions of the veins of cat embryos measuring, respectively, 16 and 25 mm. in length. Near the hilus of the kidney, each renal vein divides into two branches (fig. 5) and, in some cases, the bifurcation may even extend back to the renal collar.

The primitive postcardinal veins (*Pc.2*, fig. 5) still retain their bilateral symmetry. They unite caudally with the supracardinals in the lumbar region and, in addition to blood received from the mesonephroi and gonads, they also receive, in part, that collected by the external (*E.II.*) and internal iliac (*I.II.*) veins. Craniad, the postcardinals (*Pc.2*) also unite with the supracardinals (*Sprc.*) through the subcardino-supracardinal anastomosis (lateral portion of renal collar, *R.Col.*, fig. 5) so that the blood collected by the supracardinals and postcardinals in the lumbar region is then conveyed to the prerenal division of the postcava, on each side of the body, through the original subcardino-postcardinal anastomoses (*Subc.Pc.Anast.*, fig. 12) which constitute the ventral portions of the renal collar. (Compare figs. 5 and 12.)

As the result of this cranial and caudal union in the lumbar region between the postcardinal and supracardinal veins, a venous ring has been established on each side of the body, through which the ureter (*Ur.*) passes. This periureteric venous ring is bounded cranially by the caudal border of the subcardino-supracardinal anastomosis (*R.Col.*, figs. 5 and 8 and *Subc.Sprc.Anast.*, fig. 12), dorsally by the supracardinal and ventrally by the postcardinal vein. In the region of the renal collar the ureter (*Ur.*) lies dorsal to the postcardinal (*Pc.2*) and sex vein, while further caudad it passes ventral to the postcardinal vein.

FINAL TRANSFORMATIONS OF THE VEINS (FIGURE 6) WHICH LEAD UP TO THE CONDITIONS FOUND IN THE ADULT CAT (FIGURE 7).

The primary bilaterally symmetrical plan of the supracardinal veins in the lumbar region (fig. 5, *Sprc.*) is soon replaced by an asymmetrical one (fig. 6). This change is initiated by a reduction of the left side of the circum-aortic venous ring, involving its supracardinal component and of the portion labelled *R.Col.*, fig. 6, while the corresponding channels of the right side enlarge. This

change is finally followed by the complete atrophy of the left side of the renal collar, or strictly speaking, of the subcardino-supracardinal anastomosis of the left side.

In consequence of this change, the blood collected by the left supracardinal vein is therefore directed toward the right supracardinal through the intersupracardinal anastomoses and, together with the blood collected by the right supracardinal, now reaches the prerenal division of the postcava by way of the right side of the renal collar. Fig. 6 represents a stage in which the left side of the renal collar is undergoing atrophy, while in fig. 7, the left side of the collar has completely disappeared.

While it may be said that the right supracardinal vein is chiefly concerned in the formation of a portion of the postrenal division of the postcava, the supracardinal vein of the left side is also involved. The left supracardinal (fig. 6) does not, as one might suppose, undergo complete atrophy *in situ*, but rather is drawn into or fuses with the vein of the right side, at least in the caudal half of its extent. This portion of the postcava derived from the supracardinals (*pars supracardinalis*, fig. 7) may therefore be regarded as being formed largely through a fusion of both supracardinal veins, and not from a single vein on the right side, as is usually described to be the case, although the latter furnishes the major contribution.

It has been stated above that after the complete atrophy of the left side of the renal collar, all of the blood collected by the supracardinals in the lumbar region reaches the prerenal division of the postcava through the right side of the renal collar. One of the most interesting observations we may have made regarding the development of the veins in the cat, is that the right side of the renal collar typically enters directly into the formation of a definite portion of the postrenal division of the postcava, which we have designated the *pars renalis* (*P.Ren.*) of the postcava, on account of its relation to the entrance of the renal veins (*R.V.*, fig. 7). The manner in which this is brought about can best be illustrated by a series of actual reconstructions of the veins which show the relations that the right side of the renal collar bears to

the prerenal division of the postcava and to the supracardinal and postcardinal veins. The reconstructions referred to are represented by figs. 8, 9, 10 and 11 which are lateral views of the veins of the right side of cat embryos measuring 16, 25, 29 and 45 mm., respectively, in length.

In the 16 mm. embryo (fig. 8) it is seen that the right periureteric venous ring is still complete and that blood from the caudal region of the body can reach the prerenal division of the postcava by two routes, viz., by way of the right postcardinal vein (*Pc.2*), into which the sex veins open, and by way of the right supracardinal vein and right side of the renal collar. This latter route is the permanent one typically retained in the adult and *constitutes the postrenal division of the postcava*. In the 16 mm. embryo, from which this figure was drawn, the left side of the renal collar is also intact, so that blood from the left side of the body can also reach the prerenal segment of the postcava through a corresponding set of veins (fig. 5).

In the 25 mm. embryo (fig. 9) both postcardinal veins (*Pc.2*) have given up their caudal connection with the external and internal iliac veins and the left side of the renal collar has also completely disappeared, so that blood from the hind limbs and lumbar region of the body, now reaches the prerenal division of the postcava solely through the fused supracardinals and the right side of the renal collar. The right postcardinal vein opens into the ventro-caudal border of the renal collar (figs. 9 and 12) and returns blood to the prerenal segment of the postcava, which it receives exclusively from the right mesonephros and from the right gonad through the sex vein.

The venous arch formed by the fused supracardinals and right side of the renal collar, in figs. 8 and 9, is a marked and constant character of these veins in the earlier stages, a condition, however, which is later changed. This change consists of a straightening out of the arch formed by the supracardinals, and of an *actual elongation, in a cranio-caudal direction, of the right side of the renal collar*. Fig. 10, of a 29 mm. embryo, shows the renal collar in the process of elongation, while in fig. 11, of a 45 mm. embryo, the elongation has been completed and the collar assumed the

condition permanently retained in the adult. As a result of this elongation, the point at which the right postcardinal (*Pc.2*) opens into the renal collar becomes gradually shifted caudad, so that the right postcardinal finally opens into the postcava (renal collar) somewhat caudal to the points of origin of the right renal veins (*R.V.*, fig. 11).

The blood from the right gonad reaches the right postcardinal through the sex vein of subcardinal derivation. After the complete degeneration of the right mesonephros, the original drainage line of the right postcardinal is occupied exclusively by that of the right sex vein (figs. 8, 9, 10, 11 and 7). The original point of connection of the right postcardinal with the renal collar, although shifted caudad, is therefore retained in the adult as the point at which the postcava is joined by the right sex vein. This point, as we have seen, is the ventro-caudal border of the right embryonic renal collar. In figs. 6 and 7, the elongation of the right side of the renal collar is represented as having taken place.

Considerable variation has been found to exist in the adult cat, as regards the relation of the points at which the right sex and the right renal veins open into the postcava. This variation can undoubtedly be explained, in some cases, at least, on the ground that the extent to which the right side of the renal collar elongates in a cranio-caudal direction may differ in individual cases. The opening of the right sex vein into the postcava, caudal to that of the right renal vein is, however, now easily explained, on the basis of an elongation of the right side of the renal collar. Furthermore, it is plainly evident that the *right postcardinal vein does not, in the slightest degree, as hitherto supposed, enter into the formation of the postrenal division of the postcava which, as we have seen, is formed by the supracardinal veins (P. Sprc.) and by the right side of the renal collar (P. Ren., fig. 7).*

As far as the postcava and its tributaries are concerned, there still remain to be considered further changes regarding the right and left renal veins and the sex vein of the left side.

It has been stated above that after the migration of the kidneys has been completed, the permanent renal veins are formed. These consist at first of a right and left pair of renal veins which

extend between the hilus of each kidney and the lateral portion of the renal collar (*Subc. Sprc. Anast.*, fig. 12).

The condition which obtains on the right side of the body in the adult, appears to be brought about by the persistence of the more ventral of the two embryonic renal veins and the complete atrophy of the other (fig. 7). This single right renal vein then retains its connection with the pars renalis of the postcava which is formed from the right side of the renal collar (fig. 7).

The relations of the postcardinal vein, into which the sex vein opens, and of the two embryonic renal veins to the renal collar are originally the same on both sides of the body (figs. 5 and 12). When the left side of the renal collar (subcardino-supracardinal anastomosis) atrophies, however, the more ventral of the two embryonic renal veins and the left postcardinal vein continue to retain their connection with the left subcardino-postcardinal anastomosis. The result is that the latter, together with the more ventral of the two embryonic renal veins, then forms the left renal vein of the adult, while the left postcardinal vein, after the complete degeneration of the mesonephros, serves as the pathway through which the left sex vein opens into the left renal vein (compare figs. 6 and 7).

On the basis of their development, the presence in the adult cat of two, three or even four renal veins on the same side of the body is now not difficult to explain. When more than two renal veins are present this condition is undoubtedly related to the extent to which the bifurcation of the original embryonic renal veins is involved.

It has long been erroneously stated in text-books of embryology that the postcardinal veins in the thoracic region give rise to the azygos veins. The history of the development of the azygos veins in the cat is illustrated in figures 3 to 7, inclusive, in which it is shown that they are derived chiefly from the supra-cardinals and that in the adult cat only the proximal end of the right azygos near the duct of Cuvier, is derived from the postcardinal vein (*Pc.1*).

As stated at the beginning of this paper the chief object of our investigation was to establish the normal ontogenetic plan

of the veins in the cat, with the hope that we might be able to interpret correctly the variant conditions of the venous system which arose as the result of atypical development of the veins.¹⁹ On the basis of this investigation we have therefore constructed a composite diagram (fig. 12) of the embryonic veins of the cat which make their appearance, at one time or another, during the course of ontogeny.

We have already shown in the preceding pages how some of these embryonic veins function only temporarily and then disappear, while others persist and are carried into the adult stage. When we meet with a venous variant in the adult it is therefore due, in the majority of cases, to the occurrence and persistence of some modification of the ontogenetic plan ordinarily followed by the veins, which is carried into the adult. It is also evident when such atypical conditions arise, that their explanation lies in the determination of the normal potential embryonic pathways which may have been concerned. Also, if our composite diagram of the embryonic veins is correct, we should not only be able to interpret the atypical conditions already found, but should also be able to predict those which are potentially capable of occurring in the adult cat.

On the basis of this composite ontogenetic plan of the veins we have been able to classify under 17 main *Types* the variant conditions of the postcava which may occur in the adult cat. We have also found that all of the postcaval variations thus far observed in man by other investigators, as well as by ourselves, can be classed under these same types.

If we return to the composite diagram (fig. 12) we see that the embryonic veins which typically enter into the formation of the adult postcava are the right supracardinal (*B*), the right subcardino-supracardinal anastomosis (*Subc.Sprc.Anast.*), the right subcardino-postcardinal anastomosis (*Subc.Pc.Anast.*), the inter-subcardinal anastomosis (*Int.Subc.Anast.*), the pars subcardinalis (*P.Subc.*) and the pars hepatica (*P.Hep.*) of the postcava.

¹⁹ Huntington, G. S. and McClure, C. F. W. 1907 The interpretation of variations of the postcava and tributaries of the adult cat, based on their development. Proc. Amer. Ass. Anat., Amer. Jour. Anat., Vol. 6.

On the other hand, it is plain that the persistence in the adult of the left supracardinal (*C*), or of the right postcardinal (*A*), or left postcardinal (*D*), either singly, in combination with one another, or with the right supracardinal vein (*B*) to form the postrenal division of the postcava, would constitute an atypical condition of the veins. In addition to the typical condition of the postcava, mentioned above, which we may speak of as *Type B*, there are therefore 14 other combinations potentially possible between the right and left postcardinals and the right and left supracardinals in the lumbar region, any one of which may persist in the adult and constitute a variant condition of the postrenal division of the postcava.

These *Types* are as follows (fig. 12):

1. *Type A*, persistence of right postcardinal (*A*) vein.
2. *Type AB*, persistence of right postcardinal (*A*) and right supracardinal (*B*) veins. Right periureteric venous ring.
3. *Type ABC*, persistence of right postcardinal (*A*), right supracardinal (*B*) and left supracardinal (*C*) veins. Right periureteric venous ring.
4. *Type ABCD*, persistence of right postcardinal (*A*), right supracardinal (*B*), left supracardinal (*C*) and left postcardinal (*D*) veins. Right and left periureteric venous rings.
5. *Type ABD*, persistence of right postcardinal (*A*), right supracardinal (*B*) and left postcardinal (*D*) veins. Right periureteric venous ring.
6. *Type AC*, persistence of right postcardinal (*A*) and left supracardinal (*C*) veins.
7. *Type ACD*, persistence of right postcardinal (*A*), left supracardinal (*C*) and left postcardinal (*D*) veins. Left periureteric venous ring.
8. *Type AD*, persistence of right (*A*) and left postcardinal (*D*) veins.
9. *Type BC*, persistence of right (*B*) and left supracardinal (*C*) veins.

10. *Type BCD*, persistence of right (*B*) and left supracardinal (*C*) and left postcardinal (*D*) veins. Left periureteric venous ring.

11. *Type BD*, persistence of right supracardinal (*B*) and left postcardinal (*D*) veins.

12. *Type C*, persistence of left supracardinal (*C*) vein.

13. *Type CD*, persistence of left supracardinal (*C*) and left postcardinal (*D*) veins. Left periureteric venous ring.

14. *Type D*, persistence of left postcardinal (*D*) vein.

With the exception of *Types ABD, ABCD* and *BCD*, all of the above-mentioned Types have been observed by us or by others, either in the adult cat or man. Type *ABCD*, however, has been figured by Hochstetter¹¹ as occurring in *Erinaceus europaeus*.

It is interesting to note in *Types A, D* and *AD* (fig. 12), that the lateral portion of the renal collar (subcardino-supracardinal anastomosis, *Subc. Sprc. Anast.*) does not enter into the formation of the postrenal division of the postcava, and, furthermore that an atypical condition invariably results whenever the postcardinal veins persist in the adult. This further emphasizes the fact, already mentioned, that the right postcardinal vein does not, in the slightest degree, typically enter into the formation of the postcava in the adult cat.

Three other types of variations of the postcava are met with which may result from atypical development of the embryonic veins. These are as follows (fig. 12):

15. *Absence of the Prerenal Division of the Postcava and Substitution for the Latter in the Thoracic Region, of the Right or Left or of Both of the Supracardinal (azygos) Veins, as the Direct Cranial Continuation of the Postrenal Division of the Postcava.*

The postrenal division of the postcava, in such cases, is usually formed by the right (*Type B*), the left (*Type C*) or by both of the supracardinal veins (*Type BC*). It would be quite possible, however, for the postcardinals (*A* and *D*) in the lumbar region also to persist in place of, or in combination with the supracardinal veins (*B* and *C*) but, as far as we are aware, such a condition has not been observed.

¹¹ Loc cit., Taf. 23, fig. 24.

Cases in which the prerenal division of the postcava (pars hepatica and pars subcardinalis) is wanting, are undoubtedly due to the circumstance that, for some reason or other, the embryonic liver circulation has not been tapped by the right subcardinal vein (figs. 1 and 2). Blood from the liver therefore continues to reach the heart throughout all subsequent stages of development, as in fig. 1, through the *V. hepatic communis* (*V.H.C.*) which serves as the hepatic revehent vein in the adult. In variants of this character in which the postrenal division of the postcava is formed by the supracardinal veins, the renal veins open into the latter and also, on each side of the body, the sex vein opens into the renal vein. This is due to the persistence of the lateral portion of the renal collar on each side of the body, into which the renal and sex veins open, the latter through the postcardinals, and the retention of its connection only with the supracardinal vein. In such cases the lateral portion of the renal collar does not enter into the formation of the postcava and, as the pars subcardinalis of the postcava is wanting, the ventral portion of the renal collar (subcardino-postcardinal anastomosis, *Subc.Pc. Anast.*), has not been formed, or, at least, has not been carried into the adult stage.

The occurrence of variants of this character in the adult cat and man, serves as a complete confirmation of its presence in the embryo and of the morphological unity of the supracardinal system of veins.

16. *Persistence of the Cardinal Collateral Veins (The Marsupial Type of Postcava).*

With very few exceptions among marsupials, the postrenal division of the postcava lies ventral to the aorta and its iliac tributaries which is the reverse of the conditions usually observed in placental forms. This has been found by one of the writers¹² to be due to the circumstance that the postcava in the lumbar region is formed in marsupials by a fusion of two veins which takes place ventral to the aorta, and which have been termed the *Cardinal Collateral Veins*.

¹² McClure, C. F. W., *loc. cit.*, 1906.

Veins occupying a similar position to the cardinal collateral veins of marsupials are present in the embryo of the cat. They may form an extensive plexus of vessels which connect with the supracardinals dorsally, and encircle the aorta ventrally between the renal level and the origin from the aorta of the umbilical arteries. In the diagram (fig. 12) only the more caudally situated portion of the cardinal collateral system of veins (*CC*) is shown, where they form a venous ring with contiguous venous channels, on each side of the body, through which the umbilical artery passes. These rings are very constant in character in this location and the *ventral* or cardinal collateral portion of the ring has been found to persist both in the adult cat and man, as the *sole* pathway through which blood can reach the postcardinals or supracardinals, as the case may be, from the external (*E.II.*) and internal iliac (*I.II.*) veins. Cases in which the cardinal collateral veins have persisted in the adult are very rare and we know of only three instances, two in the cat and one in man, in which this condition has been observed. In the marsupials, on the other hand, it is the ventral or cardinal collateral (*C.C.*) element of this circum-umbilical venous ring which normally enters into the formation of the postcava in this region, while the dorsal element of the ring disappears.¹³

As far as we have observed, the cardinal collateral veins are very evanescent in character and do not play any especially significant rôle in the normal transformations of the embryonic veins in the cat. For this reason we have omitted them, for the most part, from our diagrams in order to avoid complications and too much detail.

17. *Persistence of the Renal Collar in the Adult.*

We know of three cases in man and none in the cat, in which a complete circum-aortic venous ring, the embryonic renal collar, has persisted in the adult. Now that we know the potential possibilities of the veins in this region, however, other cases of this type of variant will undoubtedly be found, not only in man, but also in the cat.

Instances in the adult in which the left renal vein passes dorsal to the aorta before joining the postcaval vein are also easily ex-

¹³ McClure, C. F. W., *loc. cit.*, 1906, p. 203.

plained. This is brought about by the retention of a connection between the lateral portion of the renal collar on the left side and the supracardinal veins, and the atrophy of the anastomosis between the pars subcardinalis of the postcava and the left postcardinal vein (subcardino-postcardinal anastomosis).

The presence of multiple sex veins on one or both sides of the body, or of an anastomosis between the sex veins of opposite sides in the adult, has not proved a difficult matter to interpret, but may best be considered in detail at another time. Variants of this character are largely related, though not always, to atypical conditions of the embryonic subcardinal veins. No instance has yet been found, however, in which the continuous subcardinal channels in the lumbar region, as met with in the embryo (fig. 2), have been carried into the adult stage.

While for convenience of description we may classify the potential variant or atypical conditions of the adult postcava into 17 distinct types, we fully appreciate that combinations of these types may also occur. The circumstance, however, that we now possess a classification based upon a definite ontogenetic plan of the veins, seems to be a distinct advance over our former knowledge, as it not only permits us to interpret the atypical conditions of the postcava thus far observed, but also enables us to predict others which are potentially capable of occurring, and which still remain to be found.

COLOR SCHEME OF FIGURES

Blue: Cardinal System of Veins and their Derivatives.
Red: Subcardinal System of Veins and their Derivatives.
Brown: Supracardinal System of Veins and their Derivatives.
Green: V. hepatic communis and Ductus Venosus Arantii.
Yellow: Subcardino-Supracardinal Anastomosis (lateral portion of Renal Collar) and Renal Veins.
Lavender: Cardinal Collateral Veins.

FIGURES

Figs. 1 to 7, inclusive, diagrams illustrating the development of the veins in the cat (Ventral Views).

Figs. 8 to 11, inclusive, lateral views of reconstructions of the right side of the renal collar and of the right postcardinal, right supracardinal and right sex veins in cat embryos measuring, respectively, 16, 25, 29 and 45 millimeters in length.

Fig. 12. Composite diagram of the embryonic veins of the cat.

ONTOGENETIC DIVISIONS OF ADULT POSTCAVA (FIG. 7)

Pars Hepatica, P. Hep.	}	Prerenal Division
Pars Subcardinalis, P. Subc.		
Pars Renalis, P. Ren.	}	Postrenal Division
Pars Supracardinalis, P. Spre.		

EXPLANATION OF FIGURES

ABBREVIATIONS

<i>A.</i> , Right Postcardinal Vein (Lumbar Division)	<i>P.Hep.</i> , Pars Hepatica of Postcava
<i>Adr.</i> , Adrenal Vein (Adrenal Organ in fig. 7)	<i>P.Ren.</i> , Pars Renalis of Postcava
<i>Ao.</i> , Aorta	<i>P.Subc.</i> , Pars Subcardinalis of Postcava
<i>Az.</i> , Azygos Vein	<i>P.Sprc.</i> , Pars Supracardinalis of Postcava
<i>B.</i> , Right Supracardinal Vein (Lumbar Division)	<i>Pc.</i> , Postcardinal Vein
<i>C.</i> , Left Supracardinal Vein (Lumbar Division)	<i>Pc.1.</i> , Postcardinal Vein (Thoracic Division)
<i>C.C.</i> , Cardinal Collateral Veins (fig. 12)	<i>Pc.2.</i> , Postcardinal Vein (Lumbar Division)
<i>C.II.</i> , Common Iliac Vein	<i>Prc.</i> , Precardinal Vein
<i>C.J.</i> , Common Jugular Vein	<i>Prcv.</i> , Precava
<i>C.S.</i> , Coronary Sinus	<i>R.Col.</i> , Subcardino-Supracardinal Anastomosis or lateral portion of Renal Collar in figs. 4 and 5 and on left side in figs. 6 and 7
<i>D.</i> , Left Postcardinal Vein (Lumbar Division)	<i>R.In.</i> , Right Innominate Vein
<i>D.C.</i> , Duct of Cuvier	<i>R.V.</i> , Renal Vein
<i>D.V.</i> , Ductus Venosus Arantii	<i>Scl.</i> , Subclavian Vein
<i>E.II.</i> , External Iliac Vein	<i>Sprc.</i> , Supracardinal Vein
<i>E.J.</i> , External Jugular Vein	<i>Subc.</i> , Subcardinal Vein
<i>G.</i> , Gonad	<i>Sub. Pc.Anast.</i> , Subcardino-Postcardinal Anastomosis
<i>Hep.Subc.Jct.</i> , Hepato-Subcardinal Junction.	<i>Subc.Sprc.Anast.</i> , Subcardino-Supracardinal Anastomosis
<i>I.II.</i> , Internal Iliac Vein.	<i>S.V.</i> , Sex Vein
<i>I.J.</i> , Internal Jugular Vein	<i>Ur.</i> , Ureter
<i>Int.Subc.Anast.</i> , Intersubcardinal Anastomosis.	<i>V.H.C.</i> , Vena Hepatica Communis
<i>K.</i> , Kidney (Metanephros)	
<i>L.In.</i> , Left Innominate Vein

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