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SYMPOSIUM ON THE DEVELOPMENT AND STRUCTURE OF THE LYMPHATIC SYSTEM.*

I.

The Anatomy and Development of the Jugular Lymph Sacs in the Domestic Cat (Felis Domestica).

BY

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With 17 Figures.

Prior to the meeting in 1907 the writers made an extensive study of the development of the veins of the cat in order to explain from an embryological standpoint the large series of venous abnormalities which had been collected by them in the preceding years. In the course of this investigation they were impressed by the circumstance that the main lymphatic channels not only developed in close relation to the veins, but also observed, as did Lewis in the rabbit, that many of the embryonic veins appeared to be actually replaced by lymphatics in the later stages of development. A marked reciprocal relationship also appeared to exist between certain embryonic venous channels undergoing atrophy and the developing lymphatics, in the sense that as these venous channels gradually atrophied spaces were formed outside their intima which, subsequently, through fusion and growth, invaded the territory, wholly or in part, formerly occupied by the veins. On account of this reciprocal relationship between veins and lymphatics the writers[1] advanced the view, at the meeting in 1907, that the main lymphatic channels of the cat begin as extra-intimal spaces along the course of

* The following nine papers were read at the twenty-third session of the Association of American Anatomists, Chicago, January 1, 2 and 3, 1908.

[1] American Journal of Anatomy, Vol. VI, 1907.

embryonic veins and that these spaces were not to be confounded with the mesenchymal spaces of Sala,[2] since they develop in and, after becoming confluent with each other, take up, wholly or in part, the territory formerly occupied by the veins. The sinistral position assumed in the adult by the main lymphatic drainage canal, the thoracic duct, was therefore attributed by the writers to the circumstance that the embryonic veins of the left side undergo a more extensive atrophy than those of the right.

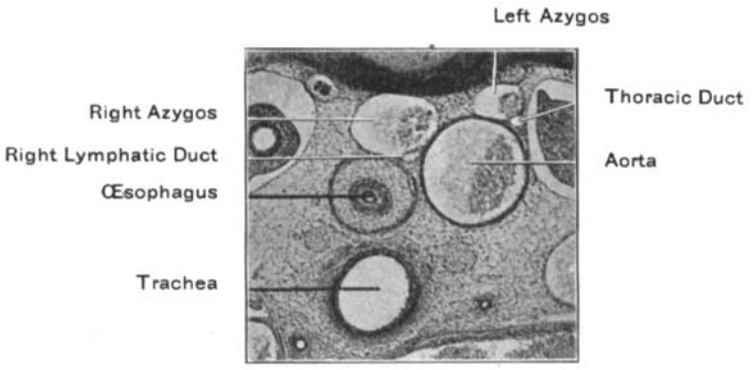

FIG. 1

Two of the many examples which might be cited in favor of the reciprocal relationship which exists between the developing lymphatics and embryonic veins which are undergoing atrophy are the relations which the right lymphatic and thoracic ducts bear to the thoracic azygos (supracardinal)[3] veins during the different stages of development, as well as the history of the partial atrophy of the postrenal division of the left supracardinal vein and its replacement by a lymphatic.

Fig. 1 represents a section taken through the anterior thoracic region of a 16 mm. cat embryo in which both azygos veins are of large

[2]Richerche n. lab. di anat. norm. d. r. Univ. di Roma, Vol. VII, 1900.

[3]Huntington and McClure, Amer. Jour. of Anat., Vol. VI, 1907. "A bilateral and originally symmetrical venous channel develops dorso-medial to the primitive postcardinal vein by longitudinal anastomoses between somatic postcardinal tributaries. This secondary vein channel forms what we have termed the supracardinal system of veins. It extends from the level at which the posterior limb veins open into the postcardinals to a point cephalad where it joins that portion of the postcardinals which alone persists to form the anterior end of the adult Azygos. Between these levels the supracardinal veins enter into the definite organization of both the adult post-cava in its

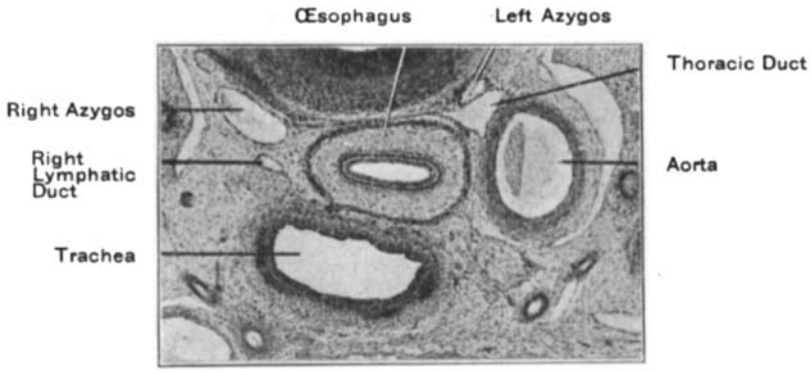

FIG. 2

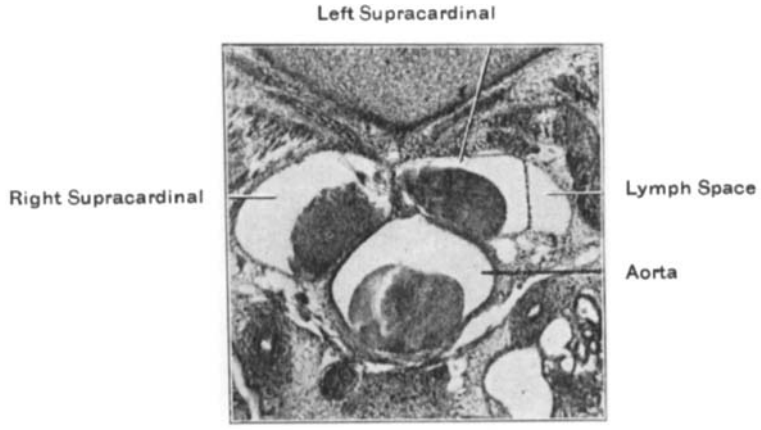

FIG. 3

size and in which the right lymphatic and thoracic ducts are small and lie in close contact with, but outside the intima of the veins. In a more advanced embryo (25 mm., Fig. 2), in a section taken through

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 in our interpretation the supracardinal veins are not in any sense merely synonyms for the dorsal limb of the peri-ureteric ring described by Hochstetter and others as surmised in the discussion following the presentation of our paper, but comprise a continuous and morphologically uniform system of longitudinal vein channels contributing, as above outlined, to the establishment of the adult condition in both the post caval and in the azygos areas."

the same region, the left azygos vein is much smaller than the right, since it has already undergone atrophy in correlation with the establishment of a permanent right-sided azygos termination. In comparing these two stages it is seen that the thoracic duct is much larger than the right lymphatic duct in the 25 mm. embryo and that it actually

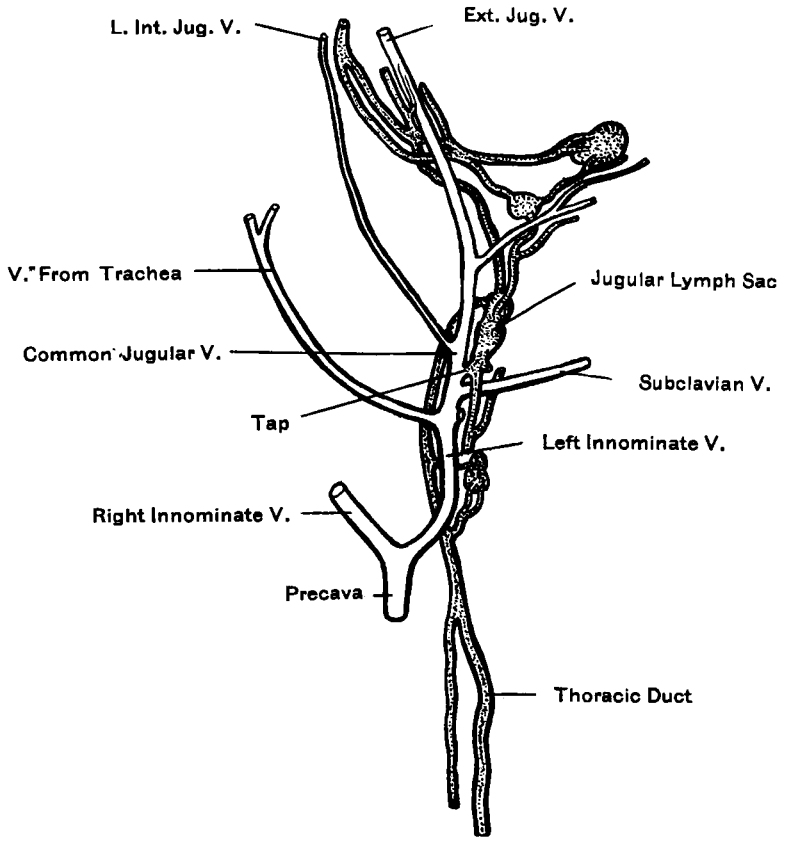

FIG. 4

encroaches upon the space formerly occupied by the now almost atrophied left azygos vein, although it still retains the same extra-intimal position with respect to the vein as in the 16 mm. embryo.

In correlation with the atrophy of the ureteric ring portion of the left supracardinal vein, since the vein of the right side, for the most part, persists as the postrenal division of the adult postcava, well

defined and clear-cut spaces are frequently met with which occupy a part of the territory formerly occupied by the vein, but which are completely separated from the latter by a partition. These spaces, which are very prominent in a 35 mm. embryo (Fig. 3), are without doubt lymphatic in character, since they are continuous forward with the thoracic duct.

Although we were and are still convinced that the principle of replacement of certain embryonic venous channels by lymphatics is cor-

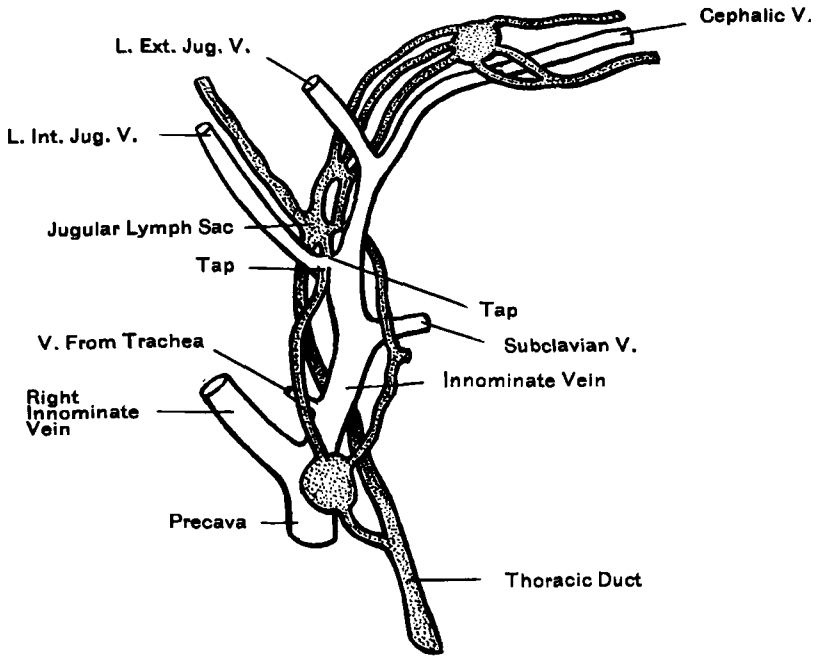

FIG. 5

rect, we were not prepared at the time of the meeting of 1907 to show conclusively that in some cases this replacement may not have been of a secondary character and that these extra-intimal spaces may not have been derived primarily from the veins. Since this meeting, however, we have made a detailed investigation of the development of the jugular lymph sacs of the cat and, so far as these elements of the lymphatic system are concerned, have proved conclusively, to our own satisfaction, that they are derived from the veins. On the other hand, as far as our

observations extend, we have been unable to find any valid evidence, in the sense in which the jugular lymph sacs are developed, regarding the venous origin of the lymph spaces and lymph vessels which are formed independently of the jugular lymph sacs and, since a proper interpretation of these spaces and vessels gives the keynote to the correct ontogenetic conception of the lymphatic system as a whole, it may be fairly stated that their genesis requires a most careful investigation.

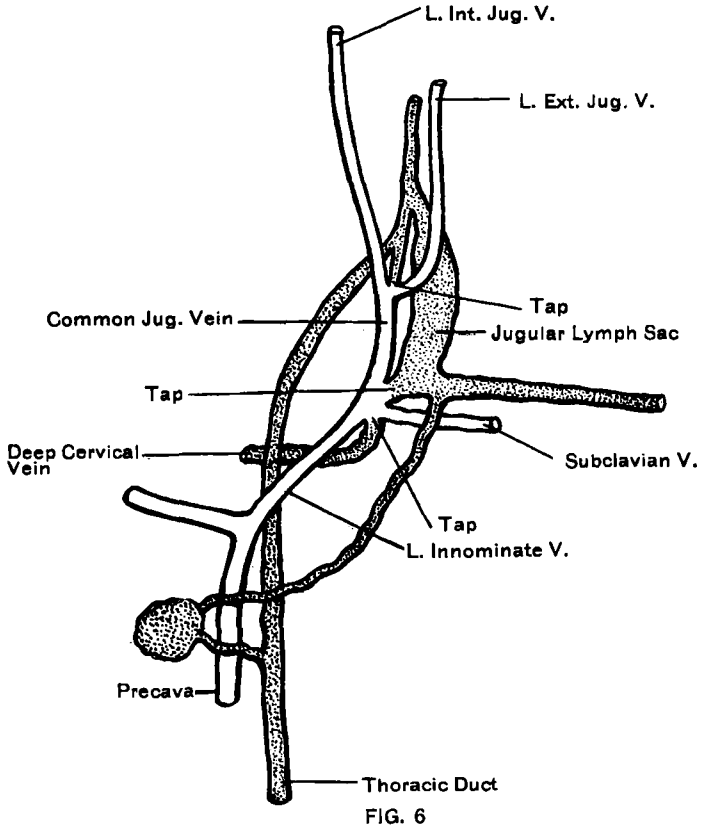

FIG. 6

3. The thoracic duct, in common with anterior end of the jugular lymph sac, may open into the veins at the point of confluence of the external and internal jugulars and, in addition to this, the posterior end of the lymph sac may also open into the veins at the common jugulo-subclavian junction, as in 1. In this case the subclavian vein may also receive an independent lymphatic vessel from the deep cervical region (Fig. 6).

The Lymphatico-Venous Connections in the Adult Cat.

The thoracic duct of the adult cat has been described by Reighard and Jennings[4] as opening into the left external jugular vein at its junction with the subclavian. An examination of a number of adult cats has shown us that considerable variation may exist on the left side regarding the connection between the venous and lymphatic systems, as follows:

1. The thoracic duct may open into the anterior end of the jugular lymph sac, while the latter opens into the common jugular vein at its point of confluence with the subclavian (Fig. 4).

2. The lymph sac may be rudimentary and, after receiving the thoracic duct, open into the veins at the point of confluence of the external and internal jugulars. A lymph vessel from the thymus region may also open into the veins at the same point. The external and internal jugular veins are in this case about subequal in size (Fig. 5).

The Development of the Jugular Lymph Sacs in the Cat. (Anterior Lymph Hearts of Sabin.)

So far as known to the writers, Sabin[5] and Lewis[6] are the only investigators who have thus far studied the development of the jugular lymph sacs in mammals.

In all of the papers thus far published by Sabin she maintains that the principle involved in the development of the mammalian lymphatic system (pig) is that of continuous centrifugal growth of lymphatic ducts from four primary venous centers which bud off from the veins in the neck and inguinal regions. The anterior pair of buds constitute the anlages of the jugular lymph sacs or hearts, and in her estimation these sacs retain from the beginning their primary connections with the veins.

Lewis, who studied the development of the lymphatics in the rabbit, states that they arise not by four but by several venous outgrowths which become detached from the venous system and, after uniting with one another to form a continuous system, acquire new and permanent openings into the veins near the subclavian termination. Although

[4]Anatomy of the Cat (p. 331).

[5]American Jour. of Anat., Vol. I, 1902; Vol. III, 1904; Vol. IV, 1904.

[6]American Jour. of Anat., Vol. V, 1905.

Lewis did not describe in detail the actual derivation of the venous outgrowths which enter into the formation of the jugular lymph sacs, he is undoubtedly correct in principle and should receive full credit for his careful observations.

The present investigation is based upon the study of serial sections and a very complete series of wax reconstructions of the venous and lymphatic systems made after the method of Born. A complete series of these reconstructions was exhibited at the meeting held at Chicago in 1908.

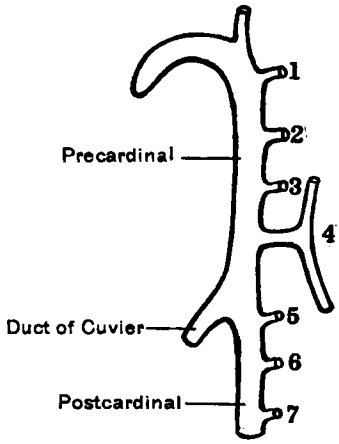

FIG. 7

Figs. 7 to 13, inclusive, are a series of semi-diagrammatic figures which illustrate the development of the jugular lymph sac of the left side, but answer as well for the sac of the opposite side, since it is developed in exactly the same manner. The stippled area indicated on the figures (Figs. 7 to 11, inclusive) represents the portion of the venous system which is subsequently split off from the main venous channels and which becomes transformed, through growth and fusion and after the evacuation of its blood contents, into the definite jugular lymph sacs.

It may be stated at the beginning that the lymph sacs present a remarkable variation as regards the details of their development, not only in different embryos of the same stage, but even upon opposite sides of the same embryo. It will therefore be necessary in this brief outline to give a more or less composite description of the conditions which may prevail at any given stage rather than those which invariably exist.

The primary principle underlying the development of the jugular lymph sacs in the cat is the separation of parallel venous channels from the embryonic veins by a process of fenestration, and the subsequent conversion of these channels into the definite lymph sacs by a process of growth and fusion.

In a 5-6 mm. embryo the process of fenestration is, as a rule, not yet evident (Fig. 7). Four fairly constant tributaries open into the dorsomedial surface of the precardinal (1 to 4) which are serially continuous with the segmentally arranged tributaries which open into the dorsomedial surface of the postcardinal vein.

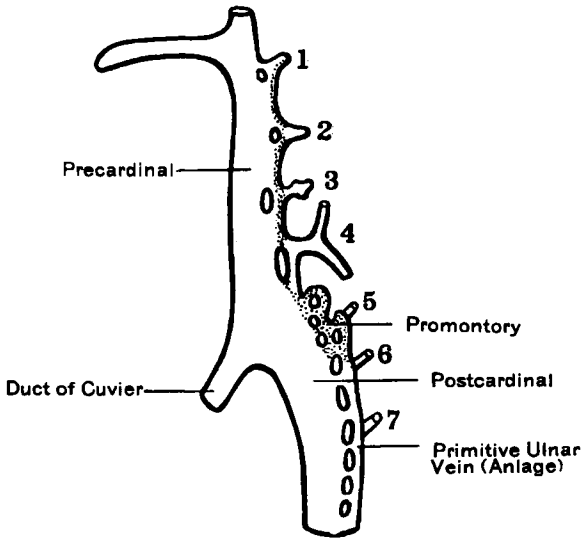

FIG. 8

In a 6.5 mm. embryo the process of fenestration is usually well advanced (Fig. 8). The fenestræ have formed along the dorsolateral surface of the postcardinal vein and are continuous forward with a similar series formed along the precardinal. The portion of the postcardinal vein involved in this process of fenestration is raised into a well-defined ridge which now projects slightly forward, in the region of the duct of Cuvier, over the precardinal vein. It is from this anterior projection of the postcardinal vein, which may be termed the "jugular promontory," that the anlages of the jugular lymph sacs are, for the most part, developed. The process of fenestration which extends along

the postcardinal vein, including the promontory, does not, at this or at any subsequent stage, involve the segmentally arranged tributaries which open into the postcardinal. This is not always the case, however, with the precardinal tributaries. The fourth precardinal tributary (4, Fig. 8) may become separated from the precardinal by a process of fenestration and subsequently open into the promontory, where it forms the first of the well defined segmentally arranged series of postcardinal tribu-

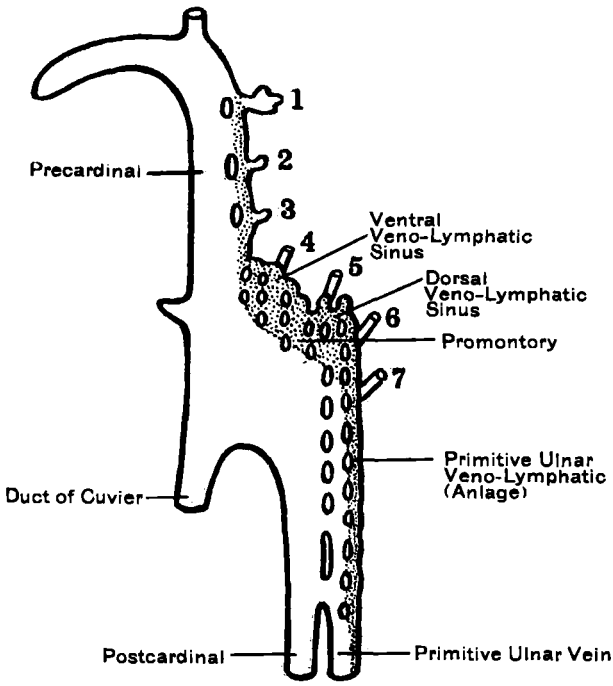

FIG. 9

taries (Fig. 9). The remaining three tributaries of the precardinal may or may not be involved in the process of fenestration. In the former case, as represented in Figs. 9 and 10, they subsequently enter into the formation of the jugular lymph sacs, while in the latter case they apparently do not. Being connected with the anterior segment of the precardinal which may (Fig. 5) or may not be (Fig. 4) transformed into a vein of importance in the adult, the fate of the precardinal tributaries is correspondingly uncertain. The anlage of the

primitive ulnar vein is already established in the 6.5 mm. embryo, but has not yet split off from the main postcardinal channel.

In a 7 mm. embryo (Fig. 9) the promontory has increased in size and the process of fenestration correspondingly more extensively developed than in the preceding stage. The two projections which extend forward from the promontory over the precardinal constitute, respect-

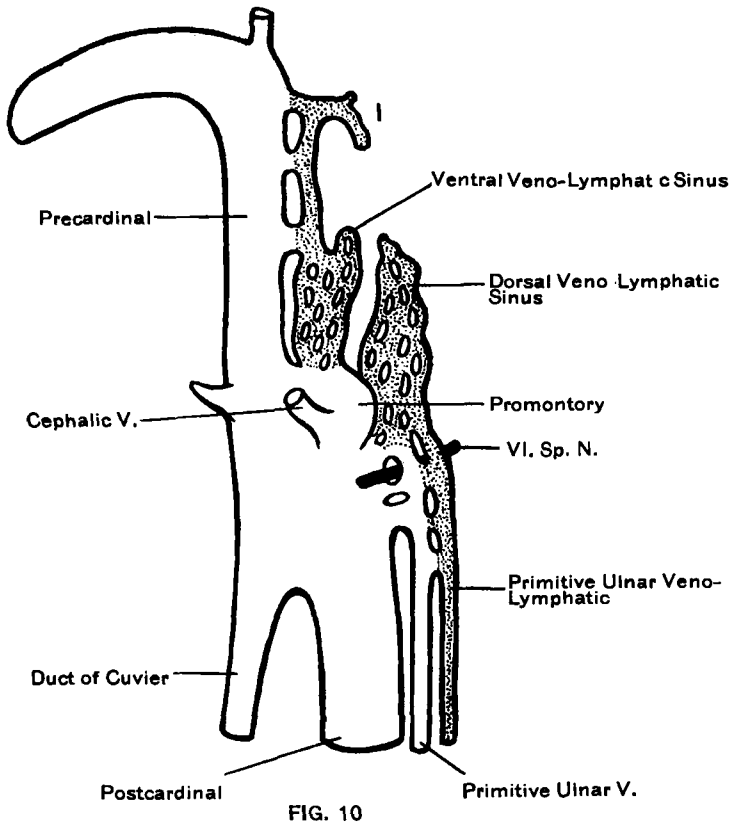

FIG. 10

ively, the dorsal and ventral divisions of the *veno-lymphatic sinuses,* a term which we have applied, for descriptive purposes, to all of the venous derivatives which subsequently enter into the formation of the definite lymph sacs, before they get rid of their blood and become separated from the main venous channels. The fourth segmental tributary of the precardinal has given up its connection with the latter vein and now forms

the most anterior or first segmental tributary of the postcardinal vein, as already described in connection with the 6.5 mm. embryo. The primitive ulnar vein has already begun to split off from the postcardinal vein, from behind forward, as a result of a confluence between the fenestræ which were formed between it and the main channel of the postcardinal vein. A new vessel which will subsequently be involved in the lymphatic system is also beginning to be split off from the primitive ulnar vein by a similar process of fenestration (anlage of the primitive ulnar lymphatic, Figs. 9, 10, 11, 12 and 13).

In an 8.5 embryo (Fig. 10) the dorsal and ventral divisions of the veno-lymphatic sinuses extend for some distance in front of the promontory and are distinctly separated from each other. This separation has probably been brought about as the result of a confluence between the fenestræ in the promontory. The dorsal division of the veno-lymphatic sinus now opens into the dorsolateral surface of the promontory in common with the primitive ulnar vein by means of a single and much constricted opening. The primitive ulnar vein has, for the most part, been split off from the postcardinal except in the region of the promontory, where two fenestræ are still retained, through one of which the sixth spinal nerve passes. The primitive ulnar veno-lymphatic sinus has also undergone a partial separation from the primitive ulnar vein, but still retains its connections in front with the postcardinal vein, as well as with the dorsal veno-lymphatic sinus. The ventral veno-lymphatic sinus may connect directly with the face of the promontory by means of a broad opening as in Fig. 10, or, by means of a much constricted opening, with the lateral surface of the promontory, contiguous to the latter's point of confluence with the cephalic vein. This ventral sinus may also connect anteriorly with the venous elements which have been split off from the precardinal vein.

The 10.5 mm. embryo (Fig. 11) is distinguished from that of the preceding stage, chiefly by the circumstance that the dorsal veno-lymphatic sinus has grown forward, dorsal to the precardinal vein, where it frequently makes a secondary connection with the venous system by anastomosing with one of the dorsal tributaries of the precardinal vein. This secondary connection with the precardinal vein often becomes much enlarged and, when such is the case, the sinus may give up its primary conection with the promontory. The ventral veno-lymphatic sinus now fuses with the dorsal sinus caudally, but no longer opens into the precardinal vein. It still retains, however, a narrow connection

with the lateral surface of the promontory contiguous to the point where the latter receives the cephalic vein. The ventral veno-lymphatic sinus, although quite variable in form, is more or less sac-like at this stage and lies upon the lateral as well as upon the dorsal surface of the precardinal vein. The primitive ulnar vein and its veno-lymphatic

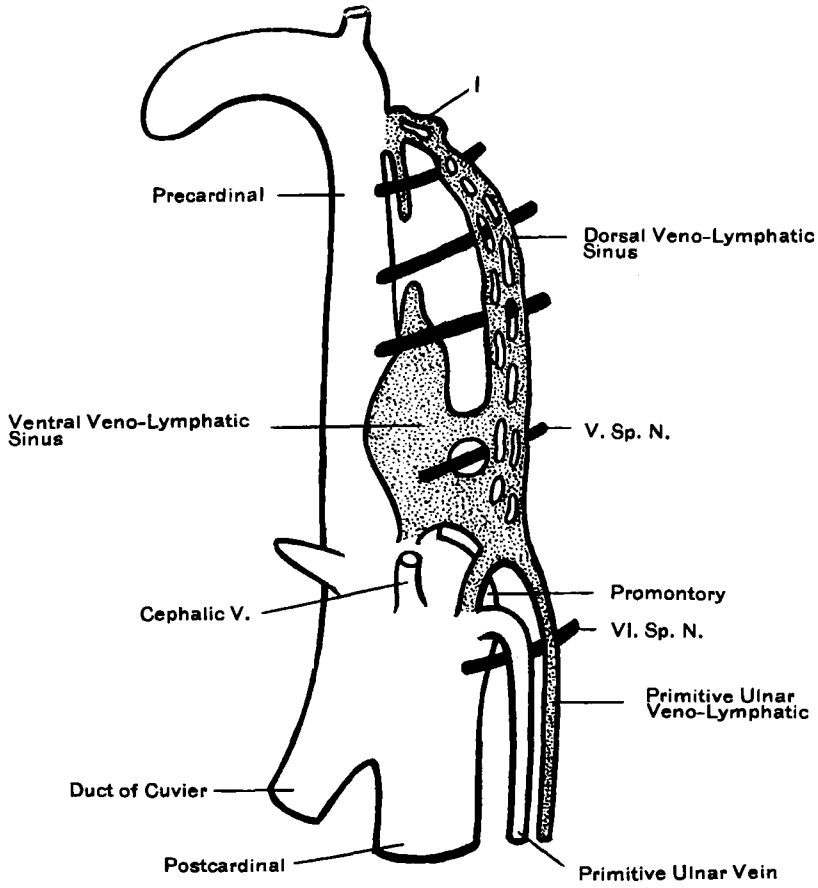

FIG. 11

derivative are entirely separated from each other. The former opens into the dorsolateral surface of the promontory, while the latter is directly continuous with the dorsal division of the veno-lymphatic sinus.

The relations which the nerves bear to the veno-lymphatic sinuses in the 10.5 mm. embryo (Fig. 11) are worthy of mention, since essentially

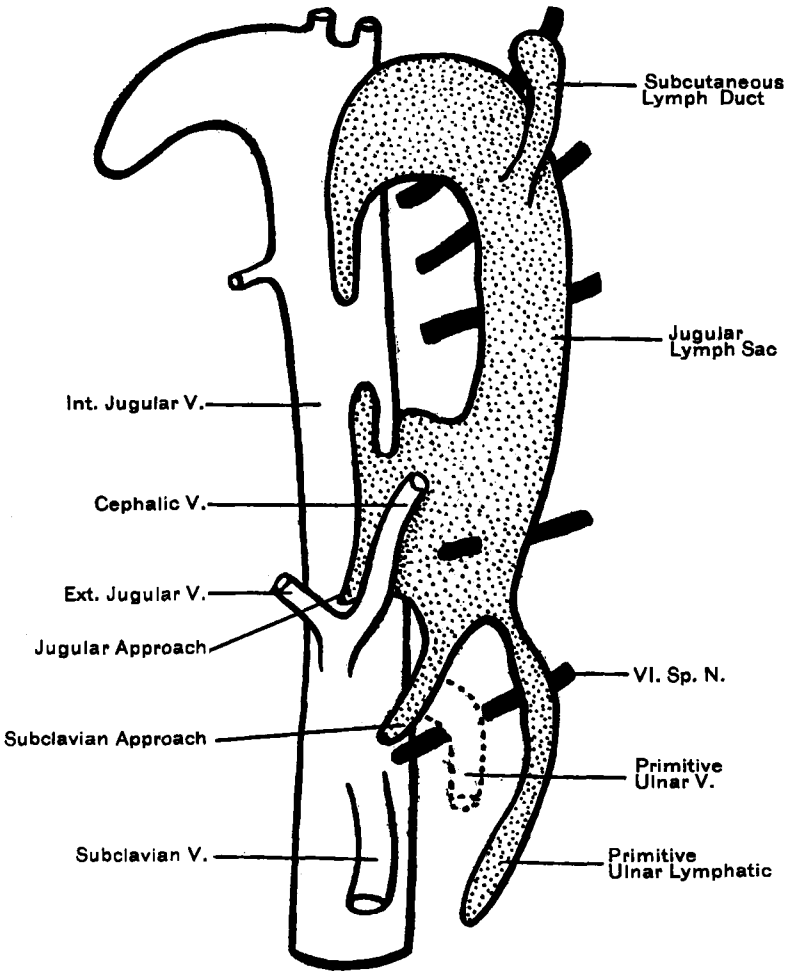

FIG. 12

the same relations are maintained in later stages after the veno-lymphatic sinuses have been converted into the definite jugular lymph sacs. The second, third and fourth spinal nerves pass laterad between the two veno-lymphatic sinuses, while the fifth may either penetrate the dorsal sinus or, as represented in Fig. 11, may pass through a foramen formed between the two.

The subsequent development of the veno-lymphatic sinuses, in stages more advanced than that last described, consists, as far as we can deter-

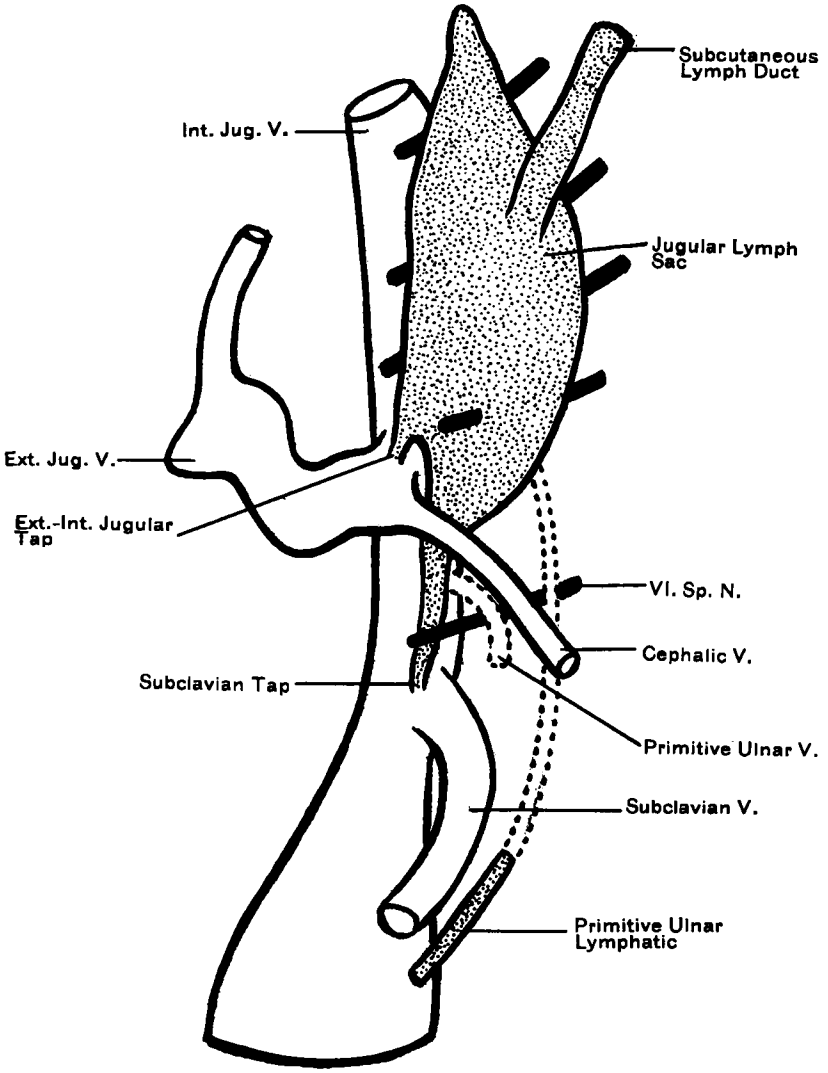

FIG. 13

mine, of a further fusion between them to form a single sac, of an evacuation of their blood contents and, finally, of their complete separation from the venous system. When these changes have taken place, one can speak of these sacs thus formed as belonging to the definite

lymphatic organization, although, practically, the only distinction that can be made in early stages (10.5 mm. embryo) between the veno-lymphatic sinuses and the definite lymphatic sac, is that one contains blood corpuscles and functions as a vein, while the other does not.

The evacuation of the blood from the veno-lymphatic sinuses appears to take place at a time when the embryos measure between 10.5 and 11.5 mm. in length. The process of evacuation is very rapid and the veno-lymphatics of the left side usually lose their blood before those of the right.

In a 10.7 mm.[7] embryo, which is represented by Fig. 12, the evacuation process has taken place and a complete separation apparently established between the veins and, what may now be termed, the jugular lymph sac. The jugular lymph sac is also quite compact in form and possesses a complicated multilocular structure. Also, although at this stage there is no observable connection between the lymph sac and the veins, the sac sends out two processes which approach and almost reach the two points at which the lymph sac often connects with the veins in the adult (Fig. 6).

These two points appear to correspond, respectively, to those at which at an earlier stage the dorsal and ventral veno-lymphatic sinuses opened into the jugular promontory (compare Fig. 12 with Figs. 10, 11 and 13) and, in view of this relation, it may be regarded as still open to question whether the lymph sac ever separates from the veins at these two primary points of connection except in those cases in which only one connection is destined to persist in the adult (Figs. 4 and 5). If a continuity exists throughout development, it is evident from our observations that the character of the connection in the 10.7 and 11 mm. embryos differs widely from that in the earlier and later stages in which its appearance is typical, unmistakable and most easily identified.

A number of other important changes have taken place in the 10.7 mm. embryo. The promontory has entirely disappeared, probably in correlation with an elongation of the vein in this region. The primitive ulnar vein has also given up its primary point of connection with the venous system and the primitive ulnar lymphatic which was derived

[7]The reconstruction from which Fig. 12 was drawn was made of an embryo belonging to the Harvard Embryological Collection (Series 474, 10.7 mm. embryo), and we take this opportunity of thanking Professor Minot for his courtesy in placing this as well as several other series of embryos at our disposal.

from the primitive ulnar vein can be traced from the jugular lymph sac into the fore-limb, where it follows the course of the veins. The subcutaneous lymph duct, which is extensively developed in older embryos, now opens laterally into the jugular lymph sac.

In the 16 mm. embryo (Fig. 13), in which, so far as the jugular lymph sac is concerned, the adult condition has practically been reached, the sac has become, through growth and fusion, still more compact and sac-like than in the preceding stages. It now connects (secondarily?) with the venous system usually at two points, as is frequently the case in the adult (Fig. 6), namely, at the junction of the external and internal jugular veins and at the subclavio-common jugular junction. Each opening into the venous system is guarded by a typically con-

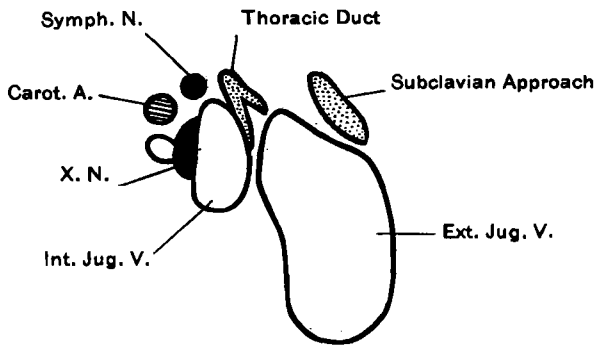

FIG. 14

structed ring valve, the character of which is illustrated by a series of camera drawings which were made of the region just preceding, as well as through the external-internal jugular tap in a 16 mm. embryo (Fig. 14, Section 234; Figs. 15, Section 237; Fig. 16, Section 240, and Fig. 17, Section 241).

Finally, with slight differences due to fusion as well as to a further expansion of the jugular lymph sac, the spinal nerves retain the same relations to the sac as in the 10.7 mm. embryo (Fig. 12). The primitive ulnar lymphatic appears to have given up its connection with the jugular lymph sac in the 16 mm. embryo, but can still be followed in the fore-limb, where it may possibly be retained in the adult as a functional vessel, although we have not been able to determine definitely that such is the case.

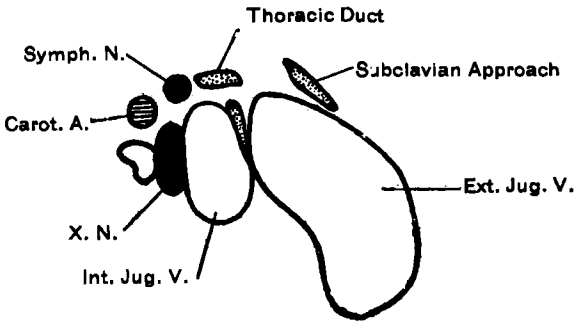

FIG. 15

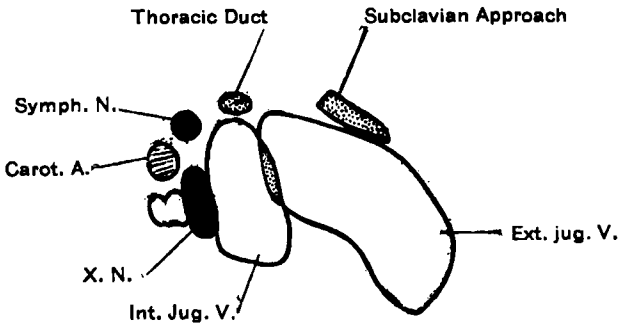

FIG. 16

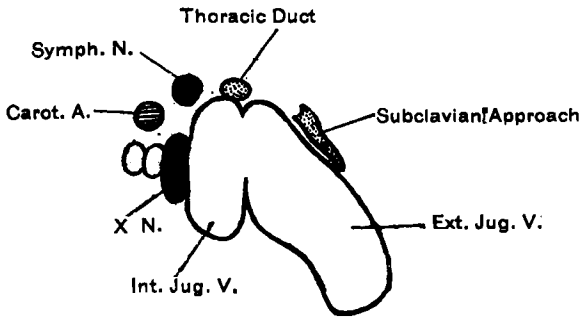

FIG. 17