Lymphatico-venous communications in the common rat and their significance

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Lymphatico-venous communications in the common rat and their significance.

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A Dissertation submitted to the Graduate Faculty of the State University of Iowa, in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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LYMPHATICO-VENOUS COMMUNICATIONS IN THE COMMON RAT AND THEIR SIGNIFICANCE.

Thesle T. Job

From the Laboratories of Animal Biology, State University of Iowa

Part I.

Lymphatico-venous communications in the Common Rat.

Introduction

Lymphatico-venous communications have been reported from time to time ever since Eustachius discovered the thoracic duct tap in 1563. Such communications have been found in a great variety of animal forms and in various parts of the anatomy. In the main, these reports have been made from data gathered while pursuing some problem other than lymphatico-venous communications and with only the purpose of recording a "peculiar condition".

Some intensive work has been done on the thoracic duct communications (group A) and several old anatomists, the foremost among them being Fohmann (11) and Lippi (12), have made extensive, but not intensive, studies of various lymphatic communications. Chas. F. Silvester (18) has carefully studied the lymphatico-venous communications at the level of the renal veins in certain monkeys, and Favaro (16) and Allen (19) have made rather exhaustive studies of regional lymphatico-venous relations, but the writer has not been able to find in the literature on this subject a single work which claims to deal intensively and extensively with the lymphatico-venous communications in any one animal species.
Such a study as this should be of value, not only in revealing the real anatomical condition, but, in explaining certain absorption phenomena, and experimental data on lymph flow. And, if the study be carried to the development of these connections, it should help to explain the origin and development of the lymphatic system and should establish what are normal and abnormal communications, as well as explain their variability in the adult.

It was with the desire of making just such a study as outlined, that the writer was privileged to undertake the task of carrying to completion the work which he presented in 1915(30). This would not have been possible had it not been for the generous support of the Laboratory of Animal Biology thru its Director, Professor Gilbert L. Houser, and, for the encouragement and advice which he and Dr. Frank A. Stromsten have so kindly given. Thanks are due, also, to Drs. H.J. Prentiss and J.T. McClintock for advice and privileges.

Material and Method

One hundred rats, Mus (Epymus) norvegicus and the white phase Mus norvegicus albinicus, have been used in this work. Because the lymphatic system in the wild rat is so much better developed than that of the captive white phase, the wild rat has been used almost entirely for the study of the lymphatico-venous communications.

A Berlin blue gelatine mass and India ink have been used as injecting media. The injections have been made thru the lymphatic nodes some distance from the point of the venous
connections so that the lymphatic vessels might be clearly distinguished from the veins and arteries, both by dissection under a binocular microscope and by observation of the flow of the injecting mass. This precaution is very necessary when the stab injecting method is used, in as much as it is possible to inject the veins from the nodes as well as the lymphatic vessels.

An attempt has been made to keep the specimens and the injecting mass at the normal body temperature while injecting. Illuminating gas, ether and chloroform have been used as the killing agents. Preference has been given to gas, because there is evidence that material killed in this way shows a higher percentage of lymphatico-venous communications.

Results

**Inferior vena cava communications.** Forty-eight per cent of the cases injected thru the lumbar nodes or posterior to them, showed connections with the inferior vena cava just anterior to the lumbar nodes. The tap was not from the node directly, but from the lymphatic vessels which lead anteriorly along the vena cava to the renal region. There was usually one tap, and, in the greater number of instances, that one was from the lymphatic vessel on the left side of the vein. In a few instances, while in the act of injecting the system, where the lymphatic vessels did not form a plexus between the nodes and where the connection was on the ventral side of the vein, the mass was seen to leave the main lymphatic channels
and enter the vein thru a short lymphatic connection; thus giving a very definite demonstration of the presence of a lymphatico-venous communication. However, in the majority of cases showing venous connections at this point, a complicated lymphatic plexus is formed and the tap is on the ventro-lateral aspect of the vein. In such cases it is necessary to make a dissection under a binocular microscope to discover the venous connection.

**Ilio-lumbar communications.** Only two cases were found where a branch given off the main lumbar lymphatic trunk on the right side connected with the ilio-lumbar vein. Both of these instances, however, were observed while the injecting mass was flowing, so their reality was very definite.

**Renal vein communications.** Barely eight per cent of the material showed renal vein communications that could be satisfactorily demonstrated. In a large number of cases a lymphatic vessel branched off the main system about one centimeter posterior to the left renal vein and ran outward toward the hilus of the kidney, but only occasionally was it possible to demonstrate its connection with the vein. This branch was never observed on the right side, but in four cases, where the right lumbar lymphatic trunk continued its course separately from the left, up to the level of the cisterna chyli, a small tap into the right renal vein was found.
Portal vein communications. In about twenty-seven percent of the animals, portal vein communications were found. The injecting mass was started through the most distal node, in the region of the ilio-caecal valve. In those specimens presenting a portal vein communication, a large branch was given off of the main lymphatic channel of the mesentery about seven millimeters from the cisterna chyli, which ran along the portal vein a short distance and then connected with it. The main mesenteric channel continued on to the cisterna chyli. In two instances the mass was watched as it flowed along its course to the venous connection.

Subclavian vein communication. Not so much attention has been given to subclavian connections because they are commonly considered to be the only venous communications of the lymphatic system; but, twenty-four cases have been worked out carefully to determine the exact condition of these taps. In all instances both the right and the left communications were present. The tap was into the subclavian vein; on the left side usually external to the internal jugular vein, but frequently external to the external jugular; on the right side, always external to the external jugular. The tap was single in all instances.

Remarks

It will be observed that all the lymphatico-venous communications found are located in three well defined regions;
the posterior end of the inferior vena cava or iliac region, including the ilio-lumbar communications; the renal region, including the portal vein communication; the subclavian region, right and left sides. It will also be noticed that the iliac and subclavian communications are more constant than the renal.

The significance of these three regions and of the variability of the connections will be considered later, but let it be noticed now that the communications between the lymphatics and the veins are direct; that these communications do not pass thru lymphatic glands as Fohmann (11) considered they did in all animals having lymphatic glands. Had the communications here cited been thru channels leading directly from the nodes to the veins, little confidence could be placed in them, because of the possibility of ruptures within the nodes. All communications in this study, however, were from the main lymphatic vessels at points well removed from the nodes. Furthermore, the lymphatic vessels giving rise to these lymphatico-venous communications, always continued their course to a definitely known lymphatic point, such as the cisterna chyli, so there was no mistaking their identity.

Figure 1 will illustrate the point in question. The injection mass forced into the lumbar nodes does not all enter the inferior vena cava thru the venous tap, but some of the mass passes on anteriorly to the cisterna chyli and in some cases to the renal veins, thereby removing any doubt as to the reality of these lymphatic vessels.
There has not been a single incident in all of the injections made in this study, of the mesenteric lymphatic channels passing thru a lymphatic node just before entering the cisterna chyli or portal vein. This is opposed to the view advocated by Fohmann and held to some extent even today. In connection with H. Baum's (17) study it may be noted that the lower cervical, caudal, lumbar and cisterna nodes are the only nodes in the rat thru which the systemic lymph passes shortly before entering the veins.

The portal vein communication offers a very interesting study in its relation to experiments dealing with fat absorption from the intestine. "Experiments of this kind show that, after deducting the amount of fat that escapes absorption and is lost in the feces, the amount that may be recovered from the thoracic duct is less than that taken in the food" (20). "The amount thus carried by the thoracic duct during the period of active absorption -- -- has never been found to amount to more than sixty per cent, and is usually much less than this" (21).

The question naturally arises, what becomes of the forty per cent which is absorbed and yet does not appear in the thoracic duct? It has been suggested that the venous capillaries in the intestine take up this difference; but there is objection to this, because the accepted method of fat absorption does not accord with the present views of capillary absorption. Several studies of the fat content of the portal blood have been made in the attempt to show the presence of a
large quantity of fat there. Zawilsky (22) "found very little fat in the blood of a dog which had been fed on a highly fatty diet, and whose chyle was drawn off", while G. d'Errico (23) found that the fat content of the portal vein was always higher than the jugular during fat absorption. Heidenhain (24) did not find "any difference during fat absorption in the percentage of fat present in portal and carotid blood".

More recent studies show that, there are different kinds of fats with different degrees of absorbability, and, because the older methods of blood analysis did not distinguish between these fats, such results are unreliable. Therefore, it appears that the above studies, while true with the methods used, did not present the real condition.

It should be noted in this connection, that a portal blood analysis with the latest methods would not present the true status of the fat content, unless the presence or absence of a lymphatico-venous communication be determined and the blood to be studied drawn proximal to this communication.

The difficulties encountered in connection with the method of fat absorption are overcome when the presence of a lymphatic portal connection is recognized. The greater portion of the chyle absorbed which does not go thru the thoracic duct must surely enter the portal vein thru the lymphatic portal connection. Physiological experiments which indicate this connection, are those of Munk, Starling, Leathes and Bloor.
Munk (25a) found fat droplets in the liver after feeding animals a fatty meal. Starling (25) discovered that by ligating the thoracic duct, the absorption of fat was impeded but not abolished. Further, while the thoracic duct was ligated, a fatty meal was fed; it was found that a considerable portion of the fat was absorbed but the percentage of fat in the blood was not raised. Leathes (26) says "anyone who has determined the amount of fat in the liver in a long series of animals that are presumably normal will have been struck by figures occasionally obtained that are very different from those that may be taken as normal average figures for this organ, different even from those that would be abnormally high for other organs. Taking one series of about forty animals - - - five out of the series, or 1 in 8, gave an analysis double or more than double this amount" (2 to 4 per cent).

These are significant facts in connection with the proof of a lymphatico-venous communication between the mesenteric lymphatics and the portal vein. The report of Leathes is especially noteworthy here, because it suggests that twelve and one-half per cent of his series had well developed lymphatic portal connections. It would appear from Starling's experiments that the liver controlled the freeing of the fat passing thru it. This supposition is confirmed by Leathes who concludes that "the liver has after all something to do with the fat absorbed from the intestine" (26), which he sug-
gests later on, to be the synthesizing of the fat preparatory to its utilization in metabolism.

W.R. Bloor (27) who has perfected methods of fat detection in the blood, and, who has made careful studies with these newer methods, is inclined to agree with Leathes's hypothesis and offers further material to substantiate it.

The conclusions of these experiments further support the belief in a lymphatic portal connection. But there is one condition not yet explained. In those specimens not having a lymphatic portal communication, what becomes of the forty per cent of chyle? This can be definitely explained only by careful examination of the chyle in the thoracic duct of specimens which are known to have or not to have a portal connection. An examination of the chyle in a series of animals would doubtless show a variability in the amount of the fat found, much as Leathes secured in the examination of the liver. Bloor has already found that the upper limit of sixty per cent, ordinarily accepted, is really seventy per cent. May this not be still higher in those animals without a portal vein connection?

A careful study of such a series should show, according to the thesis here maintained, that there is a large variability in the quantity of fat passing thru the thoracic duct, which should accord with the presence or absence of the lymphatic portal connection. Also, such a study should show whether the physiological condition of the animal, other than pathological cases, had anything to do with the variability
of the quantity of fat in the thoracic duct.

As has been indicated, it was observed in killing the specimens that those killed by illuminating gas showed a higher percentage of lymphatic-venous communications than those killed with ether or chloroform. This suggested that there might be other physiological factors which influenced the demonstration of venous communications. Consequently, thereafter, special attention was given to the general physical state of the animals at the time they were killed. As a result of this attention, certain conditions of interest to this work were observed.

Pathological conditions always showed the lymphatic nodes of the involved region to be greatly enlarged, while venous communications were seldom revealed outside the subclavian region. Pregnant females, within a few days of delivery, always showed two or more venous connections besides the thoracic duct taps. The most satisfactory results of the whole study were obtained in pregnant females. The degree of activity of the rats just before killing and the length of time lapsing between feeding and killing were factors that entered most strongly. Real active rats from the wild state or those in which the chyle was flowing, almost always presented at least one venous communication exclusive of the subclavian connections. Of course, injections made immediately after killing gave much better results than those which were delayed.

The point maintained here is not that these physiological conditions create the lymphatico-venous communications, but,
that they are factors which must be taken into consideration when such a study is being made, in as much as they may influence the response of the lymphatic vessels to the injection mass. It may be that these communications are normally always present; the inability to demonstrate them being due to the physical and physiological conditions existing at the time of the injection.

There is no correlation apparent between the number and position of the venous communications in any one specimen. All communications may be present in the same specimen or any combination thereof.

Conclusions

From this study of the lymphatico-venous communications in the rat, it may be concluded:

First, that there are certain definite regions in which venous communications of the lymphatic vessels are found, namely: the iliac, the renal and the subclavian.

Second, that the communications between the systemic lymphatic vessels and the inferior vena cava are fairly constant, those between the mesenteric lymphatic vessels and the portal vein less so, while there is a very small percentage of communications between the lymphatic channels and the renal and ilio-lumbar veins; the subclavian connections are constant, generally considered to be the only lymphatico-venous communications.

Third, that there is no evidence of the venous communication being in the lymphatic nodes, but rather, that they
Fourth, that the lymphatic connections with the portal vein offers a means of explaining the difficulties which arise in interpreting experiments on fat absorption.

Fifth, that there are physiological factors which influence the demonstration of venous communications.
Part II.

The development of the lymphatico-venous communications in the common rat.

If the lymphatico-venous communications in the adult animal are to be rightly interpreted, a study of their mode of development in the embryo is necessary; because, only by tracing step by step thru a graded series of embryos, can it be understood how such lymphatico-venous communications are established; where such communications are made normally; what conditions should be considered abnormal; and, why such communications are so variable in the adult.

It is the purpose of the second part of this paper, therefore, to present the results of a study which was made on the development of the lymphatico-venous communications of the rat, in an attempt to interpret the significance of such communications.

Material and Method

Embryos from wild rats (Mus norvegicus) have been collected until a series from 4 to 42 mm. has been completed. Only those ages concerned with the immediate problem, 8, 9, 11, 14, 16, and 18 mm., have been prepared for microscopical study. The younger stages up to 14 mm. were fixed in a solution recommended by Chas. R. Stockard (28) and stored in absolute alcohol. Embryos 14 mm. and over were fixed in Chrom-Aceto-Formaldehyde and stored in 10% formalin. All series are 10 micra thick and are stained with haematoxylin and erythrosin.
Drawings and Photo-micrographs

Figures 2 to 10 inclusive, are drawings made with a projection microscope of sections taken from 8, 11 and 14 mm. embryos, at practically the same level, - the jugular, renal and iliac regions - and are to be used in a comparative as well as an individual study.

The photo-micrographs were made by Mr. Kent of the Photographic Laboratories of the State University, and are here presented to emphasize certain important points.

Results

Embryo of 8 mm. The 8 mm. embryo furnishes a very good starting point for this particular study, because the jugular sac is in a particularly fortunate stage of development, and the areas of loose mesenchyme are sufficiently formed to offer a basis for comparative study.

The head end being in a more advanced state of development, shows comparatively large areas of loose mesenchyme. At the base of the neck and the anterior part of the thorax there is practically no loose mesenchyme, while the body wall, at the level of the kidneys, again shows an increase. Posterior to this there is no loose mesenchyme. It will be noticed that the first sac to appear, the jugular sac, is in the region of the first large area of loose mesenchyme. Figure 2 and photomicrograph a and b shows the sac at this stage. It appears in these sections as a small space next to the
anterior cardinal and at the base of the two small venous branches. The vacuolated condition of the immediate territory, with a definite endothelial lining showing in certain parts, and undefined limits in others, are characteristics found in connection with each developing sac. Photo-micrograph b, which is a higher magnification of the same area at the base of the two venous branches, shows a typical condition, which will be cited in other instances later. In this section the edge of the cardinal vein is on the lower side, one of the blood-filled venous branches leads upwards. The main part of the jugular sac is to the left of this branch and has a definite boundary, excepting a small place on the left side. Just to the left of this unlined place in the sac, is seen a smaller, partially lined space, with two unlined projections directed toward the main sac. Leading upwards from the upper part of the main sac, is a long, narrow space, lined throughout, except for the small lip of three or four mesenchymal cells projecting inwards from the wall of the small blood vessel on the one side and the loose mesenchyme on the other.

This condition gives undoubted evidence of the recent breaking down of the mesenchyme between the long, narrow space and the main sac. The remnant of the wall has not as yet been completely absorbed. To the left, the mesenchyme is breaking down between the main sac and the smaller space, indicated by the unlined projections from both the sac and
the space. A venous capillary is noticed just below the small space. A series of fifty sketches were made in both directions from this section to determine whether the spaces united with each other elsewhere. They did not.

Attention should be called to the two small venous branches which pass outwards and upwards thru this lymphatic sac. They are traceable only a short distance beyond the vacuolated area in this embryo and have only one anastomosis, which has the appearance of disintegration.

In the renal region, fig. 3, there is only slight indication, above the aorta, of the appearance of a loose mesenchyme, while at the periphery such an area is well defined. The iliac section, fig. 4, shows about the same stage of lymphatic development as the renal.

Embryo of 11 mm. A very noticeable increase in the area of the loose mesenchyme thru out the whole embryo, and, the large size of the jugular sacs, are the outstanding features of the 11 mm. embryo. In the head region, fig. 5, the mesenchyme is well filled with definite channels and unlined spaces. The drawing only shows those channels which stand out prominently under low magnification. The jugular sacs are definitely lined and the vacuolated appearance of the territory has largely disappeared. The small venous branch running thru the sac should be noticed. It can be traced to the side of the spinal cord.

In the renal, fig. 6, region the area of loose mesenchyme is very large at the periphery. About the aorta and in
various places in the developing viscera there are decided areas of loose mesenchyme. The vacuolization just dorsal to the aorta is preparatory to the formation of the cisterna chyli, which gradually moves to the right of the aorta in the older embryos. Unlined spaces are found in the walls of the intestine and in the mesentery, the forerunners of the mesenteric system and the mesenteric sac. Photo-micrograph c shows the region of the mesenteric sac. A general area of loose mesenchyme with several unlined spaces and blood-filled capillaries.

The posterior part of the embryo, fig. 7, has larger areas of loose mesenchyme with several scattered, unlined spaces toward the periphery and a vacuolization of the tissue about the posterior cardinal veins (common iliacs), the beginnings of the iliac sacs.

Embryo of 14 mm. In the embryo of 14 mm. most of the organ systems have developed to such a degree that the loose mesenchymal territories are reduced to comparatively small areas. In the head region, fig. 8, these areas are very small, and the jugular sacs are very much smaller. This is due to a connection having been made with the vein. Photo-micrograph d shows the jugular tap. In this particular section the channel is not continuous, but in the following few sections the connection between the lower limb of the "Y" lymphatic channel and the small tap on the lower, right side of the vein, can be traced. The stronger wall of the tap immediately attached to the wall of the vein is significant.
The renal region, fig. 9, is merely an advanced condition of that found in the 11 mm. stage. The mesenteric sac is gradually enlarging and several spaces have appeared in the general region. Dorsal and slightly to the right of the aorta, the cisterna chyli is found, but only slightly further developed than in the 11 mm. embryo.

The iliac region, fig. 10, still presents large areas of loose mesenchyme and the sacs have enlarged to about the size of the jugular sac in the 9 mm. embryo. Photo-micrograph e shows this area. Just above the aorta and to the right of the vein, is seen one sac, lined except for a very small place at the right and left ends. Just to the right and below are seen a series of partially lined spaces. To the left of the artery and below the vein is another sac, not shown clearly in this section because it was too weakly stained.

Embryo of 16 mm. This stage is of particular interest here, because it shows the renal and iliac lymphatico-venous communications besides the jugular connection. Photo-micrograph f shows a small communication between the renal vein and the lymphatic channel which is dorsal to it. This channel can be traced posteriorly some distance, but it does not connect, in this embryo, with the iliac sac. This is the future lymphatic lumbar channel. Photo-micrograph g shows the iliac tap, at the right of the vein. Again it should be noticed that the wall of the tap at its juncture with the vein is slightly thicker than the main lymphatic channel. Photo-micrograph g shows the mesenteric sac.
Remarks

In the 8 and 11 mm. embryos venous channels were seen passing thru the jugular sac. In the 8 mm. embryo these channels were only traceable a short distance beyond the sac and showed an anastomosis which has the appearance of disintegration. The branch in the 11 mm. embryo is traceable to the side of the spinal cord, and the sac is much larger than in the 8 mm. embryo. The 14 mm. embryo shows the venous tap, a greatly reduced sac, as well as a smaller number of venous branches. The tap close to the vein has a thicker wall than the lymphatic channel farther away, really having the appearance of a venous capillary. These observations suggest that the venous connection is established thru the reabsorption of venous branch of the embryo. The venous branches in the 8 and 11 mm. embryos are not present in the 14 mm. embryos, and that part of the tap close to the vein has all the appearance of being the root of one of the earlier embryonic veins, which becoming functionless was reabsorbed as far back as the lymphatic sac, where it was transformed into a lymphatico-venous communication.

Dr. F. A. Stromsten (29) in his work on the posterior lymph heart of the turtle, describes a condition which is very similar to that which has been found in the rat. The only difference being in the state of the capillaries at the time the lymphatico-venous communications are formed. In the rat these venous branches at the time of forming the lymphatic communications are apparently in a regressive rather than
an aggressive condition. This conclusion is based on the above observations, together with the following considerations.

If the communications had been established while the capillaries were in an aggressive state it would have been in 8 mm. stage or before, while they were growing. But, the fact that the sac continues to grow as well as the capillaries until just previous to the 14 mm. stage, when the communication is demonstrable and the sac and the number of venous branches are greatly reduced, argues for the communication being established in the rat during the regressive stage of the capillaries. A further consideration brought out in connection with abnormal venous communications adds to the belief in such a method of venous connections. However, this difference in the exact method of venous communications does not lessen the force of the fact that the lymphatics sacs of the rat develop, with this one possible exception, in the same manner as the early stages of the lymph hearts in the turtle.

Normal communications. As has been noticed, there were three regions in the adult where lymphatico-venous communications were found. A study of the embryo reveals the fact that in these same three regions, the jugular, mesenteric (renal), and the iliac lymphatic sacs are found, and, that thru these sacs the lymphatico-venous communications are regularly formed. While the tap for the portal vein has not been definitely determined, there are sufficient indications that such a tap does exist, to warrant further study and a tentative acceptance of such a connection. Such a communica-
tion will doubtless be found from the mesenteric sac; (mesen-
teric) sac is preferable to renal sac because the sac is form-
ed in the mesentery, and, judging from the adult anatomy, has
a greater number of communications with the portal vein than
with the renal vein).

All of the sacs form independently of each other, and are
not normally connected with each other until at a later period
than that at which a communication with the vein is establish-
ed. In the embryos studied not an exception has been found
to this condition. Later, as the lymphatic spaces in the
region between the sacs flow together, the diminishing sacs
are connected; the iliac and mesenteric sacs with the cister-
na chyli, and the cisterna chyli with the jugular sac.

The jugular sacs are located along the cardinal-jugular
vein, with the base or posterior end of the sac on the ulnar-
subclavian vein. Normal communications would evidently be
with these veins.

The mesenteric sac lies in the dorsal part of the dorsal
mesentery, just ventral to the renal veins and that portion
of the vena cava between them, and to the left of the vitel-
line-portal vein at its anterior end. Normally it should con-
nect with some one or more of these veins. The spaces dorsal
to the renal veins, which are not yet connected with the cis-
terna chyli, and which are in the line of the future lumbar
lymphatic channel between the iliac sacs and the cisterna
chyli, may connect with the renal veins as shown previously.
The iliac sacs are found on either side of the inferior vena cava at its posterior end and along the commencement of the iliac veins. The normal venous communications should be in this immediate territory.

Abnormal connections. From time to time reports are made of various lymphatico-venous communications in which some are considered normal and other abnormal; usually only those connecting with the subclavian vein are considered normal. From what has just been said those communications with other veins than indicated, would necessarily be abnormal. Some instances reported of abnormal communications are: Wutzer (13) and Boddart (15) found the thoracic duct connecting with the azygos vein; Carl von Patruban (14) found it opening into the innominate vein; Dr. H.J. Prentiss (9) has in his unpublished notes, sketches of communications with the supra-scapular and vertebral veins, and in one case one of three taps enters the jugular vein high up in the neck. Cases of multiple taps of the thoracic duct are interesting in this connection, because they support the belief in the lymphatic connections being formed thru degenerating venous branches.

Variability of communications in the adult. The variability of the lymphatico-venous communications in the adult is evidently due to the variable relations of the degenerating venous branches and the lymphatic spaces and sacs of the embryo. If the lymphatic spaces form a continuous channel between the iliac sac and the cisterna chyli before a connection is established between the sac and the vein, evi-
dently there would be no iliac communication. If the venous communication be established first, doubtless it would remain as long as it is functional, which very possibly would be throughout life. If there are four communications with the subclavian vein, or those veins in the immediate region, it surely means that there were four equally atrophying veins in direct relation with the jugular sac, thru which this sac connected with the veins. When the connections are with more distant veins, that is, forming abnormal communications, evidently the degenerating branch from that particular vein was the one in closest relation with the lymphatic sac, or was the first to degenerate and establish a communication. The variability of the embryonic veins can thus be an important factor in the variation of the lymphatico-venous communications.

The greater variability of the portal and renal communications, is doubtless due to the greater variety of possible communications between the mesenteric sacs and the surrounding veins,— inferior vena cava, renal and portal veins.

A connection between the different sacs is guaranteed by the appearance of mesenchymal spaces all along the route of the future main channel, so, if a venous communication be made between the sac and the vein before the connecting channels are formed, which is the natural condition, the lessening of the pressure in that region would only hasten the confluence of the remaining spaces in the particular channel effected.
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Summary

The lymphatic sacs of the rat follow closely the method of development found in the early stages of the lymph hearts of the turtle, i.e., the vacuolization of the mesenchyme in the area to be occupied by the sac, and later, the confluence of these spaces to form the sac, which are connected with the veins by degenerating venous branches. These communications are found regularly in the iliac, renal and jugular regions of the 14 – 16 mm. rat embryo. Abnormal communications are evidently the result of variable venous channels and variable relations between the venous system and the lymphatic spaces and sacs, which, also, doubtless account for the variable appearance of the lymphatico-venous communications in the adult.

General Conclusion

In the rat there are lymphatico-venous communications other than those in the jugulo-subclavian region, which are developed regularly in the embryo and retained thru out life in an average of 40% of the cases. Such communications are found with the inferior vena cava, ilio-lumbar, renal and portal veins.

These communications are significant in explaining the method of development of the lymphatic system and in accounting for certain adult variations of this system.
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Key to Plate I. and II.

Photo-micrographs

a. Area about the developing jugular sac. 8 mm.
b. Higher magnification of the lymphatic sac and spaces. 8 mm.
   1. The main sac.
   2. The cardinal vein
   3. Venous capillaries from the cardinal vein.
   4. Unlined space, except is small spots
   5. The broken down wall between a space and the main sac.
d. The jugular tap. 14 mm.
d. Dorsal mesentery in 11 mm.
   1. The venous tap
   2. One limb of the lymphatic sac. Connects with 1.
   3. The area of the future mesenteric sac.
e. The iliac sac and spaces
f. The renal tap.
   1. The iliac sac
   2. The confluent spaces
   3. The aorta just at bifurcation
   4. Cisterna chyli
   5. Renal vein tap to the space just to the left.
g. The iliac tap.
h. The mesenteric sac.
   1. The iliac tap
   2. The end of the sac
   3. The mesenteric sac, with some separate spaces and the artery and vein to the left.
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DRAWINGS

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Key to Figure I.

Inferior vena cava communication in the adult.

Shows a comparatively simple net-work of lymphatic channels between the nodes and the method of communication.

Notice that the tap is from the main lymphatic channel and is connected with the other branches of the lymphatic system that it is impossible for it to be a venous branch from the venous system.
Fig. 1. Adult Tap.
Key to Figure 2.

A section thru the jugular sac of an 8 mm. rat embryo.

2. Two venous capillaries passing thru the sac.
3. Tongue anlagen
4. Nasal cavity
5. Pharynx
6. Small area of loose mesenchyme
Key to Figure 3.

Section thru the lumbar region of an 8 mm. rat embryo.
1. Loose mesenchyme dorsal to the aorta
2. Aorta
3. Mesonephros and genital ridge.
4. Right sub-cardinal vein
5. Liver.
6. Loose mesenchyme

Key to Figure 4.

Section thru the iliac region of an 8 mm. rat embryo.
1. Loose mesenchyme dorsal to the aorta
2. Mesonephros
3. Genital gland
4. Post. limb bud.
5. Iliac vein.
6. Aorta
7. Loose mesenchyme.
Key to Figure 5,

A section thru the jugular sacs of an 11 mm. rat embryo.

1. Jugular sac.
2. Anterior cardinal vein
3. Larynx
4. Meckel's cartilage
5. Tongue
6. Venous capillary passing thru jugular sac
7. Jugular sac.
Fig. 5.
Key to Figure 6.

Section thru the lumbar region of an 11 mm. rat embryo.

1. Loose mesenchyme dorsal to the aorta
2. Aorta
3. Mesonephros
4. Genital gland
5. Limb bud
6. Area in dorsal mesentary where mesenteric sac develops. See Micrograph c.
7. Liver
8. Loose mesenchyme
Key to Figure 7.

A section thru the iliac region of an 11 mm. rat embryo.

1. Loose mesenchyme
2. Aorta
3. Iliac vein
4. Limb bud.
Key to Figure 8.

A section thru the jugular sac of a 14 mm. rat embryo.

1. Jugular sac, much reduced.
2. Anterior cardinal-internal jugular.
3. Meckel's cartilage
4. Tongue
Key to Figure 9.
A section thru the lumbar region of a 14 mm. rat embryo.
1. Loose mesenchyme and cisterna chyli
2. Aorta
3. Renal vein
4. Stomach
5. Anlagen of bladder
7. Liver, in part.
6. Kidney- metanephros
Key to Figure 10.

A section thru the iliac region of a 14 mm. rat embryo.

1. Loose mesenchyme in region of iliac sacs.
2. Iliac vein
3. Loose mesenchyme.