THE VASCULAR SYSTEM IN THE KIDNEYS OF THE COMMON PORPOISE
(*Phocoena phocoena* (L.))

by

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with one plate

INTRODUCTION

Recently thorough investigations have been made on the vascular system in the human kidneys and on the kidneys of the dog, by means of the injection-method. In whales they have never been investigated in such a conscientious way, though it seems interesting to study those more thoroughfully, especially when one likes to know more about the function of this organ. These pre-eminently sea-dwelling mammals are confronted with very exceptional osmoregulatory problems, and the function of the kidneys is therefore a very important one (SLIJPER, 1962).

In the literature nowhere a good description of the vascular system of the Cetacean kidneys is found. Only a brief description of the larger vessels and the vessels surrounding the kidneys is given by some authors. It is the intention to give here a description of the complete vascular system in the kidneys of the Common Porpoise (*Phocoena phocoena* (L.)); besides the Fin Whale (*Balaenoptera physalus* (L.)) is drawn into the research where possible.

Occasionally I will compare them with the vascular system in the kidneys of the dog and the human kidneys as they were described by KÜGELGEN and PASSARGE (1960) and HAMMERSON and STAUBESAND (1961, a, b, c). The four authors mentioned can be considered as the leading ones in the research on the vascular system in the kidneys of mammals, and therefore it is very useful to draw a parallel with their results. As it is also of importance to compare the structure of the vascular system in the kidneys of the Common Seal (*Phoca vitulina* L.) with that of the Common Porpoise, comparisons will be made with the paper of GUZSAL (1958), and some material of seals studied.

When drawing a parallel between the kidneys of the dog, the seal and the porpoise it should be kept in mind that there is a great difference in shape and structure between those kidneys. The kidneys of most mammals are bean-shaped and they are found at the dorsal side in the abdominal cavity. The ureter, the vena and arteria renalis are resp. leaving and entering the kidneys in the hilus. The tissue of the kidney is composed of two parts, namely the medulla and the cortex. The kidney of mammals can be divided into several types. In the kidney of the dog we see the type in which a large number of papillae is protruding in the pelvic cavity of the kidney, the whole organ is one body without division into compartments visible from the outside. In whales, however, the kidney is divided into rather small compartments (renculi) which are clearly visible from the outside. Only one papilla is present in each renculus. The seal also possesses kidneys composed of renculi and thus there is a great resemblance between the kidneys of seals and whales; they both are multilobular organs. Multi-lobular kidneys are not restricted to whales and other sea-dwelling mammals but they are also found in Cattle, the Otter, the Bear and the Elephant (SLIJPER, 1962).

Special attention will be given to the typical systems discovered in the kidneys by KÜGELGEN and PASSARGE and by GUZSAL in resp. the dog and the seal, both systems are namely also present in the Common Porpoise and the Fin Whale.

My grateful thanks are due to the Dutch Whaling Company Ltd. and in particular to IR. L. DE WAAL, as well as to MR. W. L. VAN UTRECHT (Netherlands Whale Research Group T.N.O.) for kind assistance in collecting the material.

TECHNIQUE AND MATERIAL

The method of investigation consisted in the macroscopical study of preserved kidneys and in the microscopical investigations of injected as well as stained kidneys.

The kidneys used for macroscopical study were fixed in formalin 5%, this induced the tissues and especially the cortex to get a more crumbly structure so that it was easy to scrape away the tissue surrounding the larger vessels.

Two kinds of fluid were used for injection of the kidneys. Most material was injected with Indian ink-gelatin solution, and part of it was used for injection with V.Y.H.H. plastic. In both methods of injecting fresh kidneys were used, which were dissected from animals which were stored for at least some days in a freezing-chamber. When is was impossible to have the intact animal for some days in a freezing-chamber the kidneys were frozen apart.

This period of freezing is necessary to obtain complete injection (KÜGELGEN and PASSARGE 1960). After defrosting, the blood was washed out with Ringer solution. The kidneys were warmed to about 37°C when Indian ink was used for padding the blood-vessels, and a warm gelatin solution with 20 drops of Indian ink to the litre was injected under slight pressure. A good pressure regulator system was not available but the presure was kept at a level by which the volume of the kidneys did not increase more then it was in situ.

Kidneys which leaked were not used for investigation as it is known that leakes may lead to incorrect conclusions. When injection showed to be finished, the veins and arteries through which was injected were legatured and the whole organ was immersed in formalin 5%. The formalin causes fixation of the tissues and hardening of the gelatin. After elucidating the kidney with wintergreen-oil-benzol in a ratio of 2 : 1, sections were made with a razor and mounted for microscopical investigations.

The same preparations were made for injections with V.Y.H.H. plastic, but acetone was injected after washing the blood with Ringer. The treatment with acetone is necessary to expel the water from the organ, as water may induce too early a polymerization of the plastic.

When the kidneys were dried, V.Y.H.H. plastic was injected. Veins and arteries were legatured after injection and the organ was immersed in concentrated HC1 to macerate the tissues and to cause polymerization of the plastic. After some days the plastic cast of the blood vessels is ready for investigation. Details were mounted for microscopical studies. The method of injection was based on data given by KÜGELGEN and PASSARGE (1960) and STAUBESAND (1956, 1957).

A number of histological sections, 5 μ thick of the kidneys was stained according to the method of Crossmonn.

The material used for investigation consisted of kidneys of six Common Porpoises, two Common Seals and one Fin Whale. The Common Porpoises as well as the Common Seals were placed at my disposal by the Netherlands Whale Research Group T.N.O., they were collected in the North Sea. The Fin Whale material was collected on board of the whale factory ship ms. "Willem Barendsz" during the season 1959-1960 in the antarctic section of the Atlantic Ocean.

For injections with Indian ink three kidneys of the Common Porpoise, one of the Common Seal and one renculus of the Fin Whale were used. The injection with V.Y.H.H. plastic was applied to two kidneys of the Common Porpoise, one of the Common Seal and to one renculus of the Fin Whale. Four renculi of the Common Porpoise and two of the Fin Whale were stained according to the method of Crossmonn.

GENERAL MORPHOLOGY

The kidneys of the porpoise, and of whales in general, are composed of a number of renculi. The vessels running in these renculi and those that are concerned with the bloodsupply of the renculi, are all mentioned in diagram I. The figures before the names correspond with the figures in the depicted renculus (Fig. 1 and 4), with those in the fotographs and with those of the paragraphs below. In diagram I a primary and a secondary vascular system is distinguished. The primary system includes all those vessels which act in the secretion of urine while those vessels which are not really concerned with the secretion of urine are said to form the secundary system. As there are more vessels concerned with the urine secretion than always accepted, the two conceptions "primary" and "secundary" are only partly identical with "vasa publica" and "vasa privata".

The first problem in describing the anatomy of a whale kidney is to what part of a single kidney the renculi are to be homologized. In the renculi, lobuli are to be distinguished and the aa.interlobares branch from an other artery in the hili. Since the aa.interlobares form a connection between the aa.arcuata and the a.renalis it is evident that the a.renalis reaches the hili of the renculi. When this is correct the renculi are homologous with the lobi of a simple kidney. Some authors (HARRISON and TOMLINSON, 1955 and OMMANNY, 1932) are of another opinion on the division of multilobular kidneys; they homologize the renculi with lobuli and recognize a rather small number (5–8) of lobi in the organ. I believe

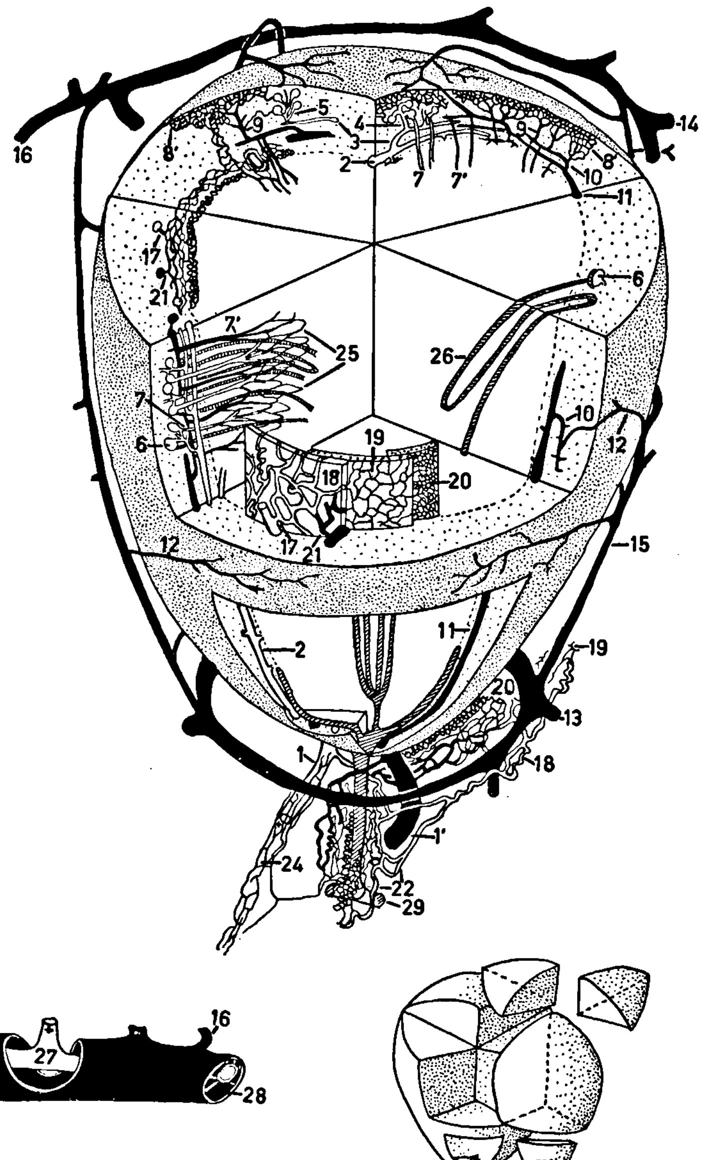

Fig. 1. Diagram of a renculus of the Common Porpoise. For explanation of figures see diagram I.

this opinion is not tenable for the Common Porpoise and the Fin Whale.

The branches of the a.renalis ending in the hili of the renculi, are commonly indicated by a number dependent on the number of bifurcations passed between the main branch and the ending of the vessel.

It is known that in the region where the a.renalis branches from the aorta, a number of variations exists in the arrangement of the vena cava and the aorta (SLIJPER, 1936). In the Common Porpoises studied, the aorta was mostly found inside the vena cava (Fig. 1), but sometimes the aorta was found partly or completely separated from the v.cava.

DIAGRAM I

Vessels:	to be found:
PRIMARY VASCULAR SYSTEM,	
A. Arterial Section	
1. a.renalis	between aorta and renculi
2. a.interlobaris	in the renculi around the pelvic cavity
3. a.arcuata	in the renculi between cortex and medulla
4. a.interlobularis	in the lobuli in the cortex
5. afferent a. of glomeruli	in the lobuli in the cortex
6. glomerulus	in the lobuli in the cortex
7. a.recta spuria	in the lobuli in both cortex and medulla
B. Venal Section (Inner Part)	
1′. v.renalis	between v.cava and renculi
11. v.interlobaris	in the renculi around the pelvic cavity
10. v.arcuata	in the renculi between cortex and medulla
9. v.stellata	in the lobuli in the cortex
8. efferent v. of glomeruli	in the lobuli in the cortex
8′. cortical plexus	in the cortex
7′. v.recta spuria	in the lobuli in both cortex and medulla
C. Venal Section (Outer Part)	
16. v. perirenalis	between v.cava and renculi
12. capsular veins	going from the renculi
13. plexus v.profundus	between the renculi
14. plexus v.superficialis	between the renculi
15. plexus interrencularis	between the renculi
SECUNDARY VASCULAR SYSTEM,	
D. Arterial Section	
17. a.pelvica	between cortex and medulla (chiefly)
18. plexus A	around the pelvic cavity (chiefly)
19. plexus B	around the pelvic cavity (chiefly)
20. plexus C	around the pelvic cavity (chiefly)
E. Venal Section	
21. v.pelvica	between cortex and medulla (chiefly)
18. plexus A	around the pelvic cavity (chiefly)
19. plexus B	around the pelvic cavity (chiefly)
22. ureter plexus	around the ureter
F. Mixed Section	
24. perivascular plexus	around the larger blood vessels
23. plexus of the capsula	around the kidney
25. medullar plexus	in the medulla
Other figures	
26. loop of Henle	in the cortex and medulla
27. aorta	in the abdominal cavity
28. v.cava	in the abdominal cavity
29. ureter	in the abdominal cavity

PRIMARY VASCULAR SYSTEM

A. *ARTERIAL SECTION in the Common Porpoise and Fin Whale.*

(1) The a.renalis runs from the aorta to the renculi and is bifurcated in a dichotomous manner. Each renculus is provided with only one branch of the a.renalis. Sometimes two or even more cavities are present in one renculus, here we are dealing with two or more renculi which coalesce. Mostly, nothing is seen form the outside of the compound character of such a renculus. The a.renalis gives off a branch to each renculus inside the seemingly singular one. This is the only place present where the a.renalis is surrounded by real kidney tissue. In a simple kidney, as found in the dog, all the branches of the a.renalis are surrounded by kidney tissue.

(1′) The vena renalis is like the arteria bifurcated in a dichotomous manner, and each renculus is provided with one branch of the v.renalis. In the porpoises investigated, only one main branch of the renal vein was found in each kidney. As reported by HARRISON and TOMLINSON (1955) more main branches of this vein are sometimes found in a certain Cetacea. From the Fin Whale no data on the number of vv.renales are available.

(2) The a.interlobaris has its origin in the a.renalis at the point where the latter enters the renculus. The aa.interlobares are almost without furcations. From these arteries the aa.pelvicae and aa.arcuatae rise. From the hilus the aa.interlobares find their way to the top of the renculus along the pelvic cavity, i.e. between the medulla and the cortex.

(3.) The aa.arcuatae give rise to the aa.interlobulares, moreover some aa.pelvicae have their origin in the aa.arcuatae. The aa.arcuatae are found in the cortex where it bounds the medulla.

(4) The aa.interlobulares lead the blood to the afferent arteries of the glomeruli. The aa. interlobulares are never branched. The afferent arteries of the glomeruli furcate from the aa.interlobulares and it should be noticed that these furcations are arranged in a dichotomous manner. Aa.pelvicae are sometimes found branching from the aa.interlobulares.

(5) In the porpoise kidneys arteriolae rectae are found to originate from the afferent arteries of the glomeruli, this is not observed in the kidneys of the Fin Whale. In the kidneys of man it is always said that these arteriolae do rise from the glomeruli; this is also found in the porpoise besides the arrangement mentioned. The arteriolae rectae penetrate the medulla as a part of the medullar plexus.

(6) The glomerulus together with the capsule of Bowman forms the renal corpuscle of Malpighi. The glomerulus is composed of a cluster of blood vessels and the capsule of Bowman is the organ collecting the urine secreted. The blood comes in the glomeruli by the afferent arteries and it leaves by the efferent vessels which are considered to be a part of the arterial system, by some authors (MAXIMOW and BLOOM, 1957). Sections injected with V.Y.H.H. plastic show clearly the construction of the plexus of the glomerulus (Fig. 2), and it is found to be similar to

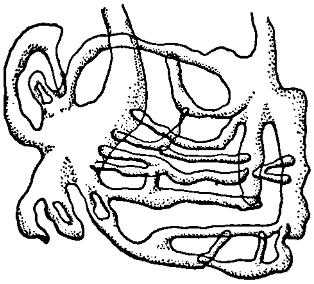

Fig. 2. Anastomoses of the efferent and afferent vessels in the glomerulus of the Common Porpoise, drawn from a glomerulus injected with V.Y.H.H. plastic.

the construction in other mammals (BOYER, 1956).

In the Common Porpoise and the Fin Whale it was found, that the branches of the afferent artery link with the branches of the efferent vessel in the glomerulus and between these branches of the afferent and efferent vessel a number of anastomoses is found. ADEBAHR (1962) states that only the juxtamedullar glomeruli are responsible for the blood-supply of the medullar plexus. This seems, however, not tenable for the Common Porpoise and the Fin Whale, as the plexus of the cortex, the plexus of the wall of the pelvic cavity and the plexus of the wall of the greater arteries in these animals have connections with the medullar plexus.

(7) The arteriolae rectae spuriae have their origin in the glomeruli or in their afferent vessels and they run down in the medulla in the direction of the papilla. They converge towards the hilus. In the medulla the arteriolae have their connections with the venulae rectae.

B. *VENAL SECTION (INNER PART) in the Common Porpoise and Fin Whale.*

All the above mentioned vessels are part of the system of the blood-supply towards the glomeruli. These vessels which drain off the blood from the glomeruli, will be discussed below. Three systems are to be distinguished by which the blood can find its way, e.g. via the plexus of the cortex to the vv.stellatae, from the glomeruli directly to the vv.stellatae or via the plexus of the medulla (the aa.rectae spuriae of the medullar plexus are discussed ahead).

(8) The efferent vessels of the glomeruli are sometimes running to the vv.stellatae but mostly they debouch into the cortical plexus, through which the blood can reach the veins. There is no possibility of switching over from one system to another, it is a stationnary situation. The blood-stream through the medulla, the third way for draining the blood from the glomeruli, is perhaps not such a stationnary one. May be the juxtamedullar glomeruli are sometimes draining through the medullar plexus and sometimes through the cortical plexus.

(8′) The plexus of the cortex in the Common Porpoise and the Fin Whale is identical with that of the dog. Blood of this plexus is drained by the vv.stellatae.

(7′) The venulae rectae run parallel to the arteriolae rectae in the medulla. The medullar plexus is composed of these venulae and arteriolae.

(9) The venae stellatae, which receive the blood from the cortical plexus, the medullar plexus and sometimes directly from the glomeruli, debouch in the vv.arcuatae.

(10) The venae arcuatae are found next to the aa.arcuatae and they debouch in the vv.interlobares. The vv.stellatae and the pelvic veins link with the vv.arcuatae. It should also be noticed that the capsular veins, which get special attention below, have their origin in the vv.arcuatae.

(11) The vv.interlobares form the last part of the venal system in the renculi before the vv.renales. The vv.interlobares run parallel to the arteries of the same name.

As has been mentioned, capsular veins start in the vv.arcuatae, such veins are unknown in mammals like the dog. This fact makes it evident that we are dealing with a second venal system in the Common Porpoise and Fin Whale kidneys next to the normal venal system. This aberrant arrangement is partly comparable with the venal system in the kidneys of seals. A nice description of this system is given by Guzsal (1958). The animals studied by Guzsal belong to *Phoca hispida* Schreber var. *ladogensis* (Nordquist). Between the venal system in the material of *Phoca vitulina* Linnaeus, studied by me, and that of the specimens studied by Guzsal, no typical differences were found.

Before proceeding with the description of the vascular system in the kidneys of whales a brief description of the venal system in the Common Seal (*Phoca vitulina* L.) will be given; this description is based on my investigations on two seals collected in the North Sea.

A number of capillaries comes out of the renculus at its top and sides, these are the so called capsular veins. They originate from the vv.arcuatae. The capsular veins debouch in the interrencular plexus, found between the renculi. This plexus is at one side in connection with the plexus venosus superficialis and at the other side with the plexus venosus profundus. The plexus v.superficialis is found at the top of the renculi, and is therefore spread over the renculi while the plexus v.profundus is situated deeper in the inner part of the kidneys where the hili are found. The blood coming from the glomeruli reaches the plexus v.superficialis via the vv.stellatae, vv.arcuatae, capsular veins and the plexus interrencularis, and perhaps sometimes via the plexus v.profundus. From the plexus v.superficialis the blood can flow into the v.cava through veins of which three are present in each animal. To my knowledge these veins have no special name. To simplify further discussions the name venae perirenales is proposed. In the kidneys of the Common Seal no v.renalis is found, and the plexus surrounding the renculi together with the vv.perirenales replace the v.renalis and the vv.interlobares. In the Common Porpoise and the Fin Whale the normal system of the vv.arcuatae, interlobares and renales is present but beside this, the venal system as found in the Common Seal is present. Summarizing it is clear, that there are three ways in Cetacean kidneys by which the blood from the glomeruli can reach the vv.arcuatae and that there are two ways by which the blood from the vv.arcuatae can flow to the vena cava.

C. *VENAL SECTION (OUTER PART) in the Common Porpoise and Fin Whale.*

(12) The capsular veins branch from the vv.arcuatae (Foto A) and perhaps sometimes from the vv.interlobares. After leaving the renculus they debouch in the interrencular plexus. Generally more capsular veins are fused together before they reach this plexus. This arrangement has to be considered as an overflow system branching from the normal vascular circuit of the kidneys. The capsular veins are always connected with the interrencular plexus and never with one of the other plexus outside the renculus.

(13) The plexus venosus profundus sinus renalis is

scattered, irregularly, around the renculi in the area of the hili. This plexus is less developed than the other two discussed below so that it is difficult to find. The only connection with other vessels is found in the junction with the plexus interrencularis.
(14) The plexus venosus superficialis sinus perirenalis is the best developed of the three we are concerned with here. The plexus receives the blood from the plexus interrencularis, and the blood is drained off by the perirenal veins.
(15) The plexus interrencularis is the plexus that receives the blood from all the capsular veins. As many of the renculi do not reach the surface of the kidneys, it is difficult to determine the build of this as well as of the other plexus. At the upper side, the interrencular plexus has connections with the plexus venosus superficialis and at the underside with the plexus venosus profundus.
(16) The vv.perirenales have their origin in the plexus venosus superficialis. Three of them are found in each animal, the first one debouches in the v.cava near the v.renalis, another one near the caudal top of the kidney and the third one between the two mentioned. HARRISON and TOMLINSON (1955) mention in the Common Seal, however, connections which are found between the vv.perirenales and other vessels which do not belong to the system of the kidneys; in the Common Porpoise and the Fin Whale these connections have not yet been found but they may exist, beside the normal connection with the v.cava. Comparing the superficial venous plexus of seals and Cetacea, it is put forward by HARRISON and TOMLINSON (1955) that the plexus is less developed in the latter and that the vv.perirenales are lacking. In my opinion this plexus is less developed indeed in the Common Porpoise but the vv.perirenales are certainly present, though they are perhaps smaller than in the Common Seal.

From the above description it is evident that there are in the Common Porpoise two ways along which the blood can reach the v.cava, therefore the Common Porpoise differs from the dog and the Common Seal in its venal system. As to the Fin Whale it is not absolutely certain, that there are vv.perirenales present, but the capsular veins present in the Fin Whale suggest, that there may be also vv.perirenales draining the blood next to the vv.renales. It is to be expected that we are here not only dealing with a difference in anatomical but also in physiological characters of the venal system. It may be supposed, that the influence of the double venal system on the blood pressure is an important one. As no closing mechanisms are found in the veins, except for the valves normally found in veins of medium caliber, it is very well possible, though not necessary, that both the system of the v.renalis and the vv.perirenales are active at the same time.

The venous plexus surrounding the renculi together with the vv.perirenales show the renculi not to have the very distinct separate character which they are usually supposed to have.

The vessels of the secundary system, which are not directly associated with the urine production, are described below. These vessels are concerned with the food supply of the tissues and the regulation of the blood pressure in several parts of the kidneys. All the blood vessels here considered as belonging to the secundary vascular system in the kidneys of the Common Porpoise and Fin Whale are identical in structure and function with those in the kidneys of the dog.

SECUNDARY VASCULAR SYSTEM

D. *ARTERIAL SECTION in the Common Porpoise and the Fin Whale.*

(17) The aa.pelvicae (Photo E,F) have their origin in the aa.renales, aa.interlobares, aa.arcuatae or in the aa.interlobulares. Consequently nearly all the arteries of the primary vascular system are in connection with the secundary system. All the plexus situated between the cortex and medulla, viz. around the pelvic cavity and around the ureter are provided with blood by the aa.pelvicae. Only the plexus of the capsula of the kidneys and the perivascular plexus have their own connections with the primary system or with vascular systems outside the kidneys.

The plexus around the pelvic cavity, between the cortex and medulla, is so closely connected with the ureter plexus ,that no defined boundary is found. In the kidneys of the dog, and in simple kidneys in general, the ureter plexus seems clearly distinguisable from the plexus of the wall of the pelvic cavity so that KÜGELGEN and PASSARGE (1960) considered them separately. I will follow them to avoid confusion.

The plexus of the wall of the pelvic cavity is composed of three different plexus running parallel to each other (Photo C; Fig. 3). These plexus were defined in literature in different ways, for the sake of simplicity I will use the indications A, B and C for the three plexus resp. situated near the cortex, between A and C, and near the medulla of the renculus.
(18) The plexus A is composed partly of offshoots of the pelvic vessels and partly of connections of these. The greater part of this plexus seems derived from the pelvic veins. The meshes of this plexus are rather

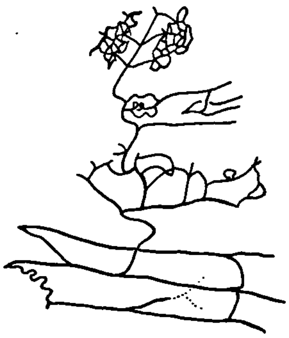

Fig. 3. The plexus of the wall of the pelvic cavity of the Common Porpoise drawn from a section injected with Indian ink.

coarse. Often twirly shaped capillaries are found. A sharp boundary between plexus A and B is difficult to find in most places. The aa. and vv.pelvicae are both connected with the plexus A.

(19) The plexus B has connections with the plexus A and with the plexus C. The meshes of this plexus are somewhat smaller than in plexus A. In the capillaries several bends are present but the typical twirly shaped vessels have almost disappeared.

(20) The plexus C, only in connection with plexus B, has very fine meshes. Capillaries with a tortuous shape are never found in this plexus. This plexus is characterized by its very great regularity.

E. *VENAL SECTION in the Common Porpoise and the Fin Whale.*

From the injected sections it is difficult to conclude which parts of the three plexus are venal and which arterial. But it seems corerct to consider the greater part of the plexus A and B as venal. KÜGELGEN and PASSARGE (1960) notice that there are relatively more vv.pelvicae than aa.pelvicae. As to the Common Porpoise and Fin Whale no counting was done for the number of these vessels, but the resemblance of the plexus studied by the authors mentioned and those in whales, permit, to my opinion, the supposition, that in the latter the same relation exists between the vv. and aa.pelvicae.

(21) The vv.pelvicae are draining the blood from the plexus A to the veins of the primary vascular system, which are the vv.renales, vv.interlobares, vv.arcuatae and the vv.stellatae. The circulation of the blood through the three plexus mentioned above, starts, consequently, in the plexus A where the aa. pelvicae deliver the blood and it ends in the same plexus A where the vv.pelvicae drain the venal blood.

(22) The ureter plexus is of the same structure as the plexus of the wall of the pelvic cavity thus built up by three plexus A, B and C (Photo D). The blood-supply is maintained by the aa. and vv.pelvicae which differ in no respect from those connected with the plexus of the wall of the pelvic cavity. KÜGELGEN and PASSARGE (1960), however, report that the aa.uereteri-cae are larger than the aa.pelvicae; in the dog therefore a difference in dimensions of the arteries connected with the two mentioned plexus is found.

F. *MIXED SECTION in the Common Porpoise and the Fin Whale.*

In this section those plexus are grouped which have no layered structure and in which the venal and arterial part are no longer distinct. The plexus of the wall of the pelvic cavity and the ureter plexus are therefore just on the line, as a clear boundary between arterial and venal provinces is not found everywhere in these plexus.

(23) The plexus of the renal capsule, around the kidneys, is composed of a single layer of venal and arterial capillaries. The blood is led directly from the aorta to the plexus and it is also drained directly into the v.cava. The meshes of this plexus are mostly composed of arteries and they are rectangular in shape. The veins in the plexus are found to be parallel to the larger arterial vessels. No twirly shaped arteries are present but a large number of strap shaped arteries is found, connecting arterial and venal vessels. Connections of the arteries and veins, supplying the plexus, with other systems not belonging to the kidneys have not been studied.

(24) The perivascular plexus is found in the kidney like everywhere in the body around the larger arteries. The vessels concerned with the blood supply of this plexus are the vasa vasorum. The plexus surrounds in two layers the wall of the arteries but there is no difference in structure between these two parts and therefore we are dealing here with a simple plexus. The very irregular meshes show from place to place some twirly capillaries and some strap shaped arteries.

(25) The medullar plexus can be considered as belonging to the primary vascular system but also partly to the secundary system. Those capillaries which are concerned with the reabsorption of water from the urine and those which take part in the food supply of the medullar plexus belong to the secundary part of the vascular system. However, only the aa.rectae

and vv.rectae have been studied and no special attention was given to the capillaries which are in close contact with the loop of Henle.

SPECIAL MORPHOLOGY OF THE PLEXUS

Large numbers of plexus are in connection with each other as shown in Fig. 4. This arrangement of plexus forms a complex overflow- and pressure-regulator system which forced me to a thorough investigation.

The plexus of the wall of the pelvic cavity varies in development from one place to another. The development is most hindered in the top of the renculi, here the plexus A and B coalesce and only the plexus C, though very small, is seen separately. The plexus A and B are braided around the interlobar arteries and veins. In the regions where enough space is available for the development of the plexus, for example in the area of the hili, between the renculi and incidentally around the ureter, the three plexus are distinguishable separately and in their full development. A rather well developed section of the plexus around the ureter is shown in photo D. Where even more room is available for the plexus, as is seen in the section photographed, twirly shaped capillaries are found, in the plexus A and sometimes in the plexus B. Capillaries which are curled like a pig's tail (Fig. 5) are found when the plexus A. occupies only little room. HAMMERSON and STAUBESAND (1961) and SPANNER (1936) give full attention to the physiological qualities of the tortuous capillaries, and they conclude that a great influence is to expect on the blood-stream. In organs which are subjected to continuous changes in volume (spleen, penis) tortuous blood vessels are adaptations to these changes. In the kidneys, however, the volume is rather constant and the tortuous vessels here are not to be considered as an adaptation in this sense. The kidneys are not the only place where tortuous arteries are found which act in the regulation of the blood-stream. A very good example of tortuous vessels regulating the blood-stream outside the kidneys is found in the arteria spermatica (WAITES and MOULE, 1960; HOFMANN, 1960). In connection with the control on the blood-stream by tortuous vessels in the plexus of the wall of the pelvic cavity, KÜGELGEN and PASSARGE (1960) also studied the valves in the pelvic veins and the musculature of the arterial wall in the dog. The valves in the pelvic veins of the Common Porpoise and Fin Whale have not been studied, but with regard to the musculature in the arteries the same conclusions may be drawn. KÜGELGEN and PASSARGE (loc. cit.) described the phenomenon: when injecting the fresh kidney of the dog, a part of the plexus of the wall of the pelvic cavity is not penetrated by the injection fluid. This incomplete injection is caused by the contraction of the muscles in the wall of the pelvic arteries. These proportionally muscle-rich capillary-walls can act in the regulation of the blood-stream in the dog, and in analogy also in the Common Porpoise, where the same incomplete injection

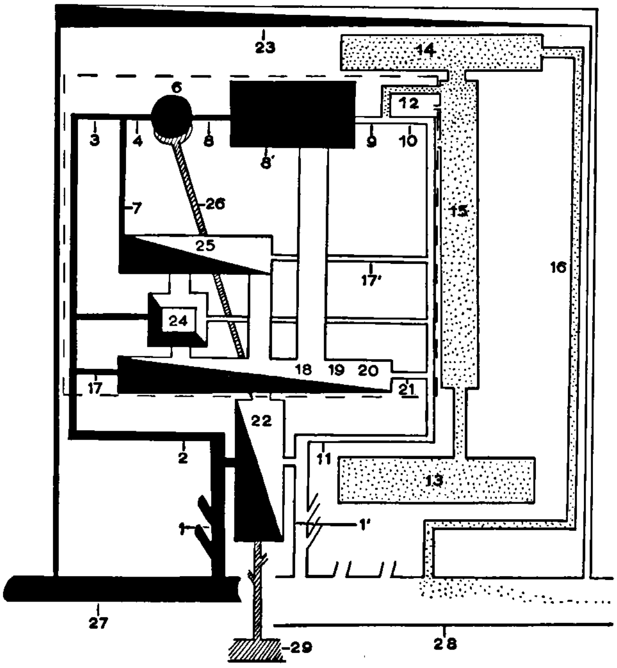

Fig. 4. Diagram of the plexus and their connections in a renculus of the Common Porpoise. For explanation of figures see diagram I.

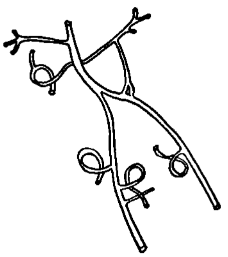

Fig. 5. Capillaries curled like a pig's tail from a section injected with Indian ink, from the plexus of the wall of the pelvic cavity (plexus A) of the Common Porpoise.

was observed. Another striking structure in the plexus is the connection of the plexus B and C. The branches of the plexus B connected with the plexus C, are running perpendicular to the latter, ending in a star-shaped pattern of capillaries of plexus C. Each "star" is composed of about five radiating arms. When the plexus are compressed a little, the feeding branches of the plexus C are no longer running perpendicular to the plexus, and the "star" shape is lost in such areas, viz. in the top of the renculus where compression is maximal.

The perivascular plexus is in connection with the plexus of the wall of the pelvic cavity and therefore it is interesting to mention that in this plexus also strap shaped arteries are present (Fig. 6). The twirly

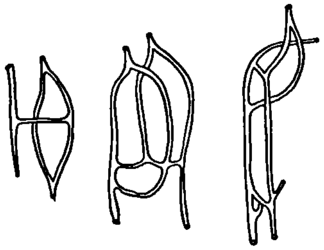

Fig. 6. Three types of strap-shaped capillaries found in the perivascular plexus of the Common Porpoise, drawn from a section injected with Indian ink.

arteries also present in the plexus are an adaptation to the continuous changes of the shape of the vessels on which the perivascular plexus is found. The strap shaped arteries are also found in the plexus of the renal capsule of the Common Porpoise and the dog as well as in the human being (HAMMERSON and STAUBESAND, 1961). As the strap shaped arteries form a connection between veins and arteries, they resemble very much arterio-venous anastomoses, but the places in the plexus where they are found refute this opinion (HAMMERSON and STAUBESAND loc. cit.).

The medullar plexus has also its connections with the plexus of the wall of the pelvic cavity. Though in this plexus no special mechanisms are found it is important to mention that the plexus acts not only in the reabsorption of water from the urine, but it may also maintain the osmotic gradient in the medulla. SCHOLANDER (1958) discusses the principle of the counter-current system in mammals and he recognizes that the loop of Henle is involved in the counter-current system. The aa. and vv.rectae run parallel and straight to the hilus of the renculus, this position is comparable with that of the nephrons and suggests, therefore, that they are perhaps also linked with the maintenance of the osmotic gradient by means of a counter-current system.

Another plexus connected with those mentioned above is the cortical plexus. This very regular plexus shows no special mechanisms and it is probable that a regulation cannot be effected by this plexus; a sharp fall of the pressure of the blood after passing the glomeruli is perhaps the only effect the plexus has.

The ureter plexus is so similar to the plexus of the wall of the pelvic cavity that it needs no further attention here.

Completely separated from the above mentioned plexus and from each other are the plexus of the renal capsule and the plexus between the capsular veins and the perirenal veins. The plexus situated between the capsular and perirenal veins is a complex of three closely connected plexus in which no special mechanisms are found.

Arterio-venous anastomoses are not mentioned in this paper, though it is known that these systems if present indicate a regulator system. In the sections injected with Indian ink and those injected with V.Y.H.H. plastic and in the material investigated histologically, no such anastomoses were found in the plexus of the kidneys of the Common Porpoise and the Fin Whale.

The anatomy of the plexus now enables to make the following speculations on their function.

The plexus of the wall of the pelvic cavity forms several connections between the arteries before they enter the glomeruli, and the veins that leave the cortical plexus, so that it may act as an extraglomerular blood circuit. The greater part of the plexus is in all probability of a venal character and the veins draining the plexus are according to KÜGELGEN and PASSARGE (1960) more numerous than the arteries, so the plexus may also act as a store for blood. The muscles in the aa.pelvicae and the tortuous arteries in the plexus may indicate that a regulation of the blood-pressure and stream in the organ is effected. As the plexus is always found where tissue containing urine borders tissues not penetrated with urine and as the plexus is a very complicated layered structure (Photo C) it is even possible that it maintains an osmotic gradient between these two types of tissue. For the ureter plexus the same suppositions can be made as for the above mentioned plexus.

The medullar plexus probably has the well known function which it has in the mammalian kidneys, i.e. the reabsorption of water from the urine and the feeding of the surrounding tissues. But, as mentioned, an osmotic gradient between the two sides of the medulla is perhaps also maintained by this plexus. Connections of the plexus with the arterial and venal system at both sides of the glomeruli are found, so the plexus may act as an extra-glomerular blood circuit. The connection of the medullar plexus with a number of other plexus and its voluminous development suggest that there is a possibility that it also acts in regulating the blood pressure in the kidneys.

The perivascular plexus is chiefly connected with the food supply of the wall of the vessels on which it is found, but beside this function it is evident that the plexus pobably acts as an overflow system which works in the co-operation with the plexus of the wall of the renal cavity (Photo B). HAMMERSON and STAUBESAND (1961 b) also discovered in the dog too the connections with other plexus, and they too suppose the plexus to have other functions than food-supply only.

The cortical plexus is so rigid in composition that it is hard to believe that the plexus itself may regulate pressure or blood stream. The connections with other plexus, however, make it possible that it has a passive role in regulation.

The plexus of the renal capsule is always considered as forming an extra-glomerular blood circuit. KÜGELGEN and PASSARGE (1960) suppose that in the dog about 60% of the blood flows extra-glomerularly through the capsula. In my opinion this is a rather high percentage for the Common Porpoise, but it may be possible.

The function of the three plexus between the capsular veins and the perirenal veins is in all probability the storing of blood. The fact that the flow off of blood from the capsular veins is restricted to the interrencular plexus and that the plexus v. profundus and part of the plexus v. superficialis are blind "sacs" which store the blood, affirm this opinion.

SUMMARY

Studying the kidneys of the Common Porpoise and the Fin Whale it was found that there is a second venal system next to the normal venal system. The arterial and venal system as found in the kidneys of the dog are present in the kidneys of the Common Porpoise without typical differences but there is also a venal system situated outside the renculi which conducts the blood from the venae arcutae to the vene cava. This system is found in the kidneys of the Common Seal but here it is replacing the system of the vena renalis which it does not do in the kidneys of the Common Porpoise.

In the kidneys of the Common Porpoise and the Fin Whale both the plexus which surround the pelvic cavity and the ureter are present and they show to be nearly similar to those described for the kidneys of the dog. Between the renculi it is found that the plexus mentioned are somewhat more developed than in the dog. The morphology of the plexus is also identical to that of the plexus in the dog, and it is supposed that their function will be also the same in the Common Porpoise and in the dog.

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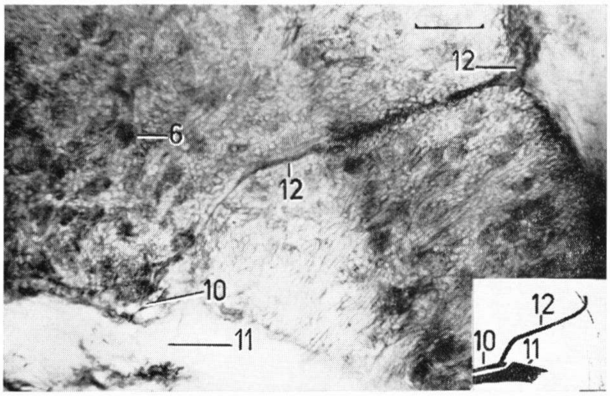

Photo A. Cross-section through the cortex of a renculus of the Common Porpoise injected with Indian ink, showing a capsular vein comming from the v. arcuata and leaving the renculus. For explanation of figures see diagram I. (Scale in 100 μ)

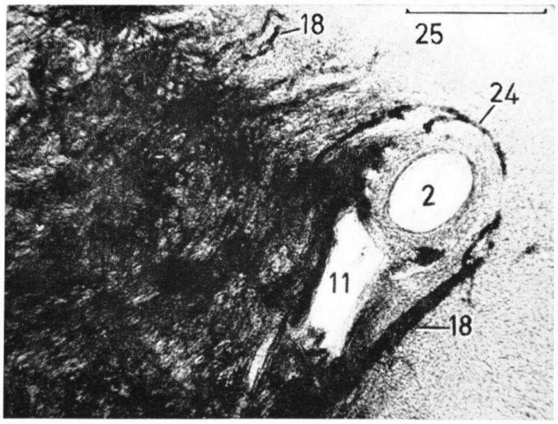

Photo B. Section through the renculus of the Common Porpoise injected with Indian ink showing the a. and v. interlobares with the perivascular plexus. For explanation of figures see diagram I. (Scale in 100 μ)

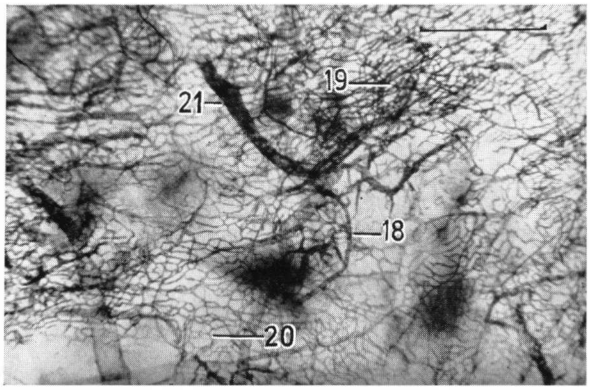

Photo C. Plexus of the wall of the pelvic cavity of the Common Porpoise injected with Indian ink. The three layers A, B and C are visible. For explanation of figures see diagram I. (Scale in 100 μ)

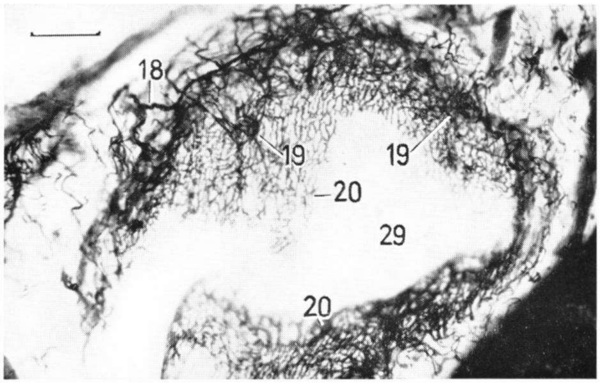

Photo D. Cross-section through the ureter and ureter plexus of the Common Porpoise injected with Indian ink. For explanation of figures see diagram I. (Scale in 100 μ)

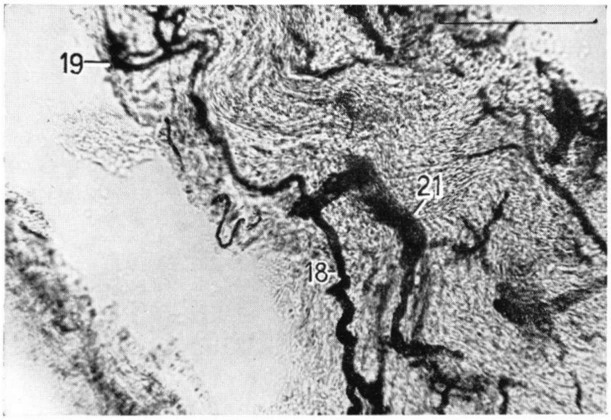

Photo E. Small section of the plexus A with a pelvic vein from the Common Porpoise injected with Indian ink. For explanation of figures see diagram I. (Scale in 100 μ)

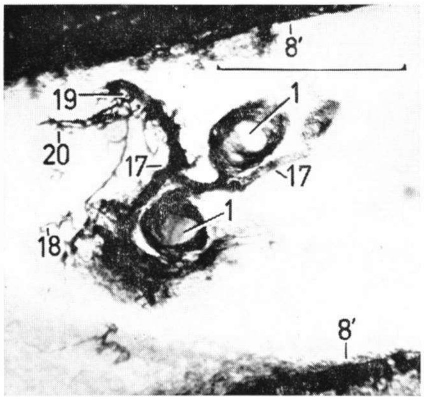

Photo F. Two arteries with pelvic arteries and the plexus A, B and C between two renculi of the Common Porpoise injected with Indian ink. For explanation of figures see diagram I. (Scale in 100 μ)