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Liver

W. H. Horner Andrews

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Liver

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1979

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Preface

The liver is not a fashionable organ for study, possibly because of the diversity of its functions. A large number of biological disciplines involve the organ: endocrinology, digestion, much enzymology, haematology, to name but a few. Only a very small number of people have spent most of their working life on the liver. Excepting for treatises by clinicians for clinicians, there have been no books written in English on the liver and a well-known expert on the liver observed of one of the best-selling of these that it has all the intellectual excitement of an army manual on weaponry.

There is a vast amount of knowledge on the liver and I have concentrated on two things. Firstly, I hope to show that the liver is a fascinating organ, though difficult to study. Second, it is time that biologists realized that the liver can be studied quantitatively, though the simple mathematics in the text can be skipped without losing the gist of the meaning. Throughout, the aim has been to deal in principles rather than with details. Fact has been included to support ideas and the greatest difficulty has been in deciding what to leave out. The book, however, at least brings together ideas and data which are widely separated both in time and in different journals.

London, 1977

W. H. H. A.

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Contents

1 Basic Morphology and some Physiological Implications

The liver is the largest visceral organ in the body and forms about 3–5% of the body weight. It probably originated as a digestive gland but is now also involved in excretion, storage and homeostasis, the maintenance of constancy in the internal environment of the body. The liver is present in amphioxus and vertebrates, but the structure called 'liver' in some invertebrates, such as gastropods, has very few properties of the vertebrate liver. There is no work on the evolution of the liver, but how it evolved can be guessed from its embryology. During development, a part of the foregut forms a blind sac, or diverticulum, which grows into the septum transversum, a mesodermal mass of cells. An intimate union takes place and endodermal cells of the gut form the biliary system with the mesoderm forming the mass of the liver. Bilirubin, a waste substance formed from the breakdown of haemoglobin, is excreted by the gut of foetal sheep after it has been conjugated to another substance. Half-way through gestation this function is taken over by the liver and after birth the gut loses the power to excrete bilirubin.

Bilirubin, or a compound giving similar reactions, is found in the 'liver' of gastropods, but this organ is near to the hind gut and is very different from a vertebrate liver. Bilirubin is not easy to detect in small amounts but in vertebrates the dyes, bromsulphthalein (BSP, also called sulphobromophthalein), indocyanine green (ICG) and rose bengal, are excreted by the same mechanism. BSP and rose bengal can be made radioactive and therefore easy to detect. Unpublished experiments by the author showed that in gastropods radioactivity was present in both the 'liver' and the gut wall after the dye had been injected into the tissue of the foot. After injection into the coelom of echinoderms, the dyes were found in the gut wall and excreted into the lumen of the gut.

It seems probable that the liver arose as a union between a secretory diverticulum of the foregut and a storage organ, and it seems likely that the hepatic portal venous system carrying food from the intestines to this organ preceded the formation of a proper liver, but this is speculation. Evolution of the liver appears to be continuing. In more primitive vertebrates, such as fish and amphibians, the liver receives blood from kidneys and peripheral tissues as well as from the gut, and non-visceral blood forms a large proportion of the blood reaching the liver. In 'higher' animals the proportion of visceral blood becomes greater and the number of non-visceral tributaries diminishes until in mammals there is a single hepatic portal vein draining the gut to the liver. This vein will, henceforth, be called the portal vein. In at least some birds there are

multiple portal veins leading from the gut and renal veins to the liver. These portal veins usually communicate with each other in the substance of the liver and the general arrangement is shown diagrammatically in Fig. 1–1. An arterial supply accompanies the portal vein and its branches within the substance of the liver.

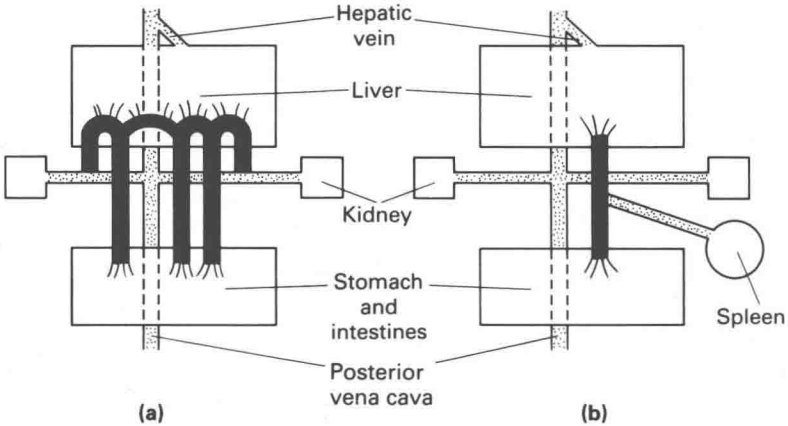

Fig. 1–1 Evolution of the hepatic portal system, highly diagrammatic. Typical arrangement in: (**a**) some birds, with multiple portal veins, (**b**) mammals. Portal veins are shaded, other veins are stippled.

In ancient times the liver was of interest for divination, and later it was considered to be the seat of the emotions (melancholic, choleric, liverish, a jaundiced view, etc.). In recent years the organ has been studied almost entirely by medics, veterinarians and biochemists. Consequently, our knowledge of the liver is confined to a few mammals (man, and domestic and laboratory animals) with a limited number of observations on other species.

1.1 General architecture, the lobule and acinus

The liver is a large, soft organ which alters in size and shape according to the amount of blood present. In mammals it is attached to the dome of the diaphragm, protected from mechanical damage by ribs, and is in the corresponding position in birds. In frogs, the anterior part is attached to the pericardium. In some animals the liver has well-defined lobes, completely separated from each other. In man it is really a single organ though anatomists divide it into several lobes, mainly on the basis of its blood supply. The surface is covered with a capsule, consisting of two layers. The outer layer is smooth, moist peritoneum. The inner is fibrous and called Glisson's capsule after the first person to describe it. The portal

vein, hepatic artery and nerves enter the liver through a circumscribed area known as the hilum, and fibrous tissue, continuous with Glisson's capsule, accompanies them, forming a kind of skeleton which, since it supports and helps to maintain the general shape of the organ, is more marked in larger animals. The histological structure of the liver depends, basically, on two large and complex vascular trees, the portal and hepatic veins which, in casts, appear as if they had been pushed into one another so that the branches and twigs of one tree lie close to, but not normally touching, the branches and twigs of the other. The portal venous branches, spreading out within the liver, are accompanied by branches of the hepatic artery, nerves, biliary and lymphatic vessels and fibrous tissue; this complex is known as a portal tract (Fig. 1–2). A variable amount of

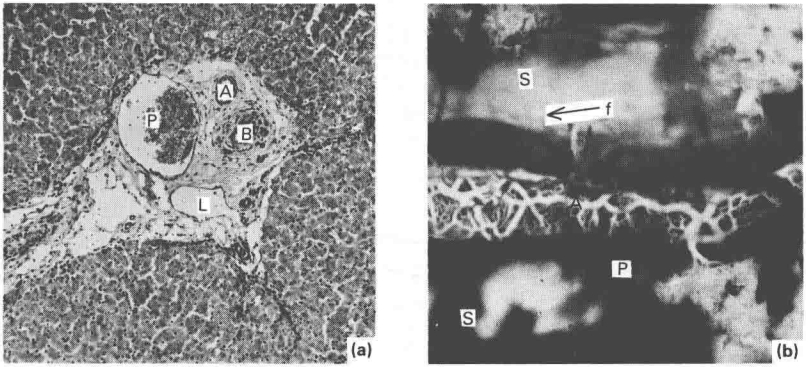

Fig. 1–2 (a) Histological section of portal tract of cat. A, branch of hepatic artery. B, bile duct surrounded by small blood vessels. L, lymph space. P, branch of portal vein. (b) Latex cast from guinea pig. The lace-like vessels are around the uninjected bile duct. A and P as in (a). S, sinusoids. f, radicular portal vein (see Fig. 1–6).

fibrous tissue accompanies the hepatic vein. The space between the two trees is filled with hepatocytes between which run small blood vessels – the sinusoids. Formerly, histologists described 'cords' of liver cells running from portal to hepatic areas, a situation which appears to exist from the appearance of histological sections, but casts of the blood vessels show, quite clearly, that sinusoids burrow their way between liver cells, branching and anastomosing as they converge upon the hepatic vein. In mammals and many other species the sinusoids are separated from each other by endothelium and a single hepatic cell, and ELIAS (1949) calls this arrangement of hepatocytes 'plates'. The plates form walls to the sinusoids and are sometimes called muralia, which are two cells thick in birds. The liver rather resembles an 'organized sponge' with the holes as sinusoids and the walls as liver plates.

Many concepts of the liver such as that of the *lobule* come from experts who have studied the liver in two-dimensional sections. By searching a section it is nearly always possible to find a typical hepatic lobule, illustrated in Fig. 1–3. It can be likened to a wheel, about 1 mm across, with the central hepatic venous drainage vein for the axle and the sinusoids running into this vein as spokes joining the axle. In the circumference of the wheel are several portal tracts, usually three or four, and branches of vessels in these tracts run tangentially in the periphery of the lobule, later dividing into the sinusoids which drain into the central vein. In the pig, fibrous tissue joins neighbouring portal tracts and when cut in the proper place, provides a definite rim to the wheel or lobule.

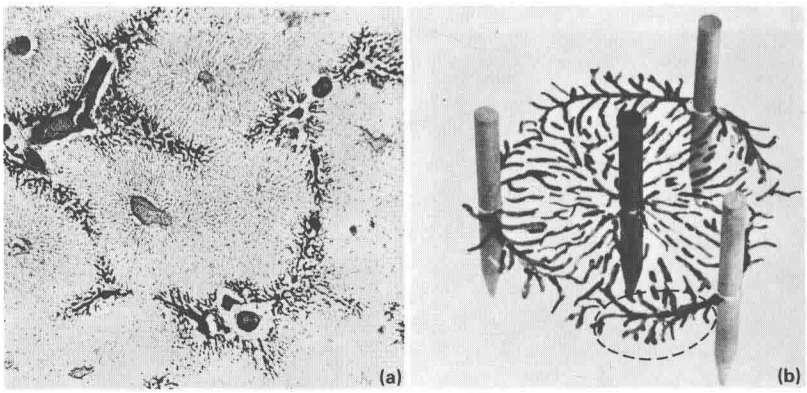

Fig. 1–3 The liver lobule. (**a**) Histological section of a rat liver taken immediately after an intraportal injection of india ink. (**b**) Model of a lobule, drawn on a transparent sheet. Three portal tracts surround and run parallel to a central hepatic vein. An acinus is outlined (– – – –) in (**b**).

However, the concept of liver lobules is less than helpful, for it gives a false impression of the structure of the organ. Hepatic veins and portal tracts do not often run parallel to each other, but cross at all angles and the lobule is seen only when adjoining hepatic and portal veins run parallel and the plane of the section is at right angles to the axes of these vessels. Figure 1–4 gives a demonstration of why generations of students have had difficulty in finding 'typical' lobules. It is almost impossible to find lobules in the livers of birds and frogs. RAPPAPORT (1958) has given the most apt description, resurrecting the term *acinus* for the basic unit, though the hepatic acinus is unlike the acinus of such glands as the pancreas and is the area immediately around one of the vessels (venules) which leaves the portal tract to supply hepatocytes. These small venules usually contain some arterial blood and run towards a neighbouring portal tract, but peter out before reaching more than half-way. They give

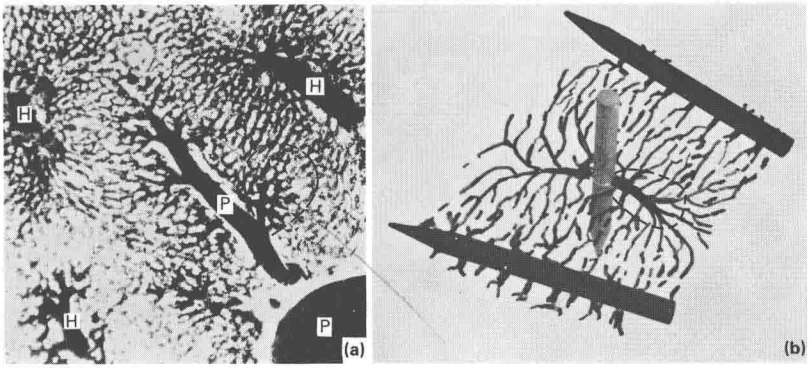

Fig. 1–4 Liver acinus. (**a**) Section of rat liver with blood vessels outlined with india ink. H, tributary of hepatic vein. P, branch of portal vein. (**b**) Model drawn as in Fig. 1–3 with two diverging hepatic tributaries and a portal tract with its axis in another plane. Acini are outlined (– – – –) in (**a**) and (**b**).

off sinusoids which run to hepatic veins, branching and anastomosing *en route*. One of the chief distinctions between descriptions of lobules and acini is that the former gives the impression of a regular, continuous structure which requires a host of parallel supply vessels, whereas the acini are discrete, though they may occur close together. The nature and amount of various enzymes in hepatocytes depend upon the distance from the supply vessel: those cells first supplied are the best nourished, whereas those which receive blood last, mostly situated near the hepatic veins, are the most liable to suffer damage. They are the first to die when the blood is insufficiently oxygenated (hypoxia) in heart failure – the centrilobular necrosis described by pathologists. The architecture of cells between portal and hepatic veins depends upon the presence of a reticular framework and if it is damaged, orderly regeneration of the liver becomes impossible. The arterial venous supply of hepatocytes is separate in the penguin which cannot be considered to have either acini or lobules.

1.2 Hepatocytes

The main cells of the liver are variously known as hepatocytes, liver parenchymal cells, liver cells and polygonal cells. Details of their structure are given in text books of histology and pathology, and a hepatocyte is illustrated in Fig. 1–5. The shape is variable, and the name polygonal cell arose from the appearance in histological slides of fixed tissue. Usually two or three aspects of the cell face blood vessels (the sinusoids), and these aspects possess microvilli which are protected from erythrocytes by the sinusoidal lining. Most of the rest of the cell is usually in close contact with other hepatocytes, but near the sinusoids the cells diverge slightly from

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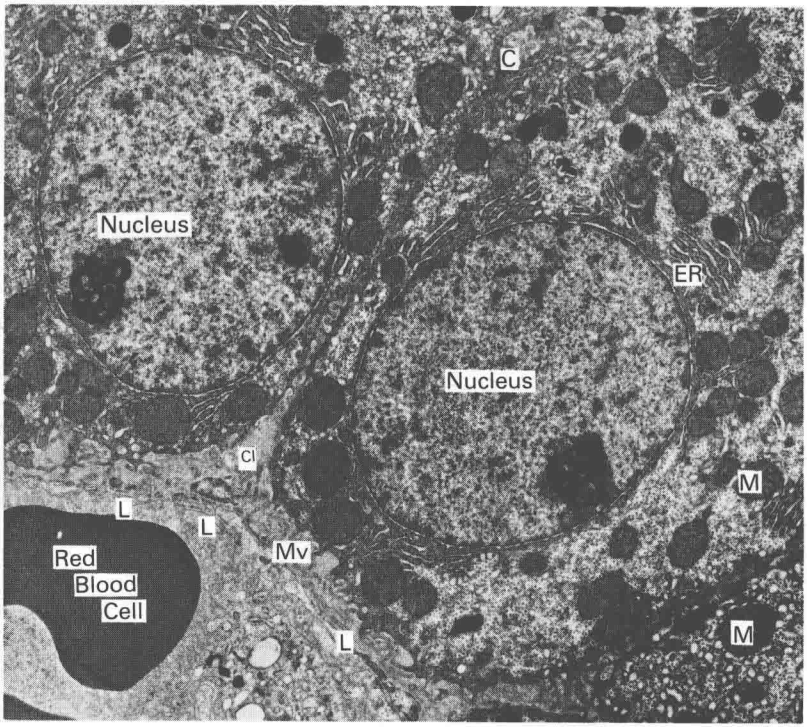

Fig. 1–5 Electron photomicrograph of human liver (courtesy of Miss J. Broadbent). Only major features are marked. C, canaliculus with microvilli; ER, rough endoplasmic reticulum; Cl, cleft between hepatocytes; M, mitochondria; Mv, microvilli; L, lining of sinusoid. A sinusoid lies in the bottom left-hand corner.

each other, forming small spaces in which extracellular fluid can collect.

In general, hepatocytes are smooth where they are in contact with each other but minute tubes, bile canaliculi, run in trough-like depressions between cells and these tubes are lined with microvilli. The canaliculi form a branching network, running between hepatic cells, which opens into the bile duct. Rough and smooth endoplasmic reticula, mitochondria and lysosomes are more abundant than in most cells and some substances, including alcohol and long-acting barbiturates, increase the amounts of enzymes and rough endoplasmic reticulum present, a process known as induction and which may be of great medical importance.

There is an electrical potential difference across the cell membrane, the interior of the cell normally being about −40 mV with respect to the

exterior. The resting potential is altered by adrenaline, noradrenaline and glucagon, substances which affect glucose metabolism, but little is yet known of this aspect of liver physiology.

1.3 Sinusoids

The functions of the liver depend not only upon the great metabolic range of hepatocytes, but also upon the properties of the cells that physically separate hepatocytes from blood. The two main cell types are endothelial and Kupffer. The endothelial cells are similar in many respects to those of other organs but contain pores, which vary in size up to 10 nm in diameter. In most mammals there is no basement membrane, but one is present in the calf and mouse. Endothelial and Kupffer cells are now considered to be of different origin. The Kupffer cells form a very important part of the liver, but are not peculiar to this organ and are normally considered in books on the reticulo-endothelial system. A great number are present in protozoal diseases, such as malaria and kala azar. They are intensely phagocytic, and between them the phagocytes of liver and spleen ingest 90% of particulate matter after it has been injected intravenously. Being in the bed of the portal vein they are well situated for removing any organisms or particulate matter which may pass through the intestinal wall and they produce unconjugated bilirubin from old and battered erythrocytes which they engulf.

Between the walls of the sinusoid and the microvilli of the hepatocytes is a narrow sheath-like zone, the perisinusoidal space, first described by MacGillivray in 1867 and frequently called the space of Disse. The wall of the sinusoid appears to be highly permeable to the crystalloids and albumin of plasma, and probably also to globulins and it prevents blood cells from damaging the microvilli on hepatocytes. Nerves have been described in this space by some workers but others disagree.

1.4 Blood supply

The arrangement of blood vessels in the liver is complicated and is shown diagrammatically in Fig. 1–6. The majority, but not all modern workers in the field, agree with the broad aspects of the diagram, and all the vessels shown have been photographed. The anatomy of the microvessels is virtually unknown other than in mammals. Many methods of study have been used. One of the early ones was to inject vessels with gelatine containing pigment particles and examine thick, cleared histological sections. Other methods include use of X-rays after injection of contrast media, microscopic examination of the edge of the liver in life and the use of serial sections of the fixed organ with and without injection of vessels. Perhaps the most informative single method is to produce vascular casts with latex or similar material and then digest the liver tissue

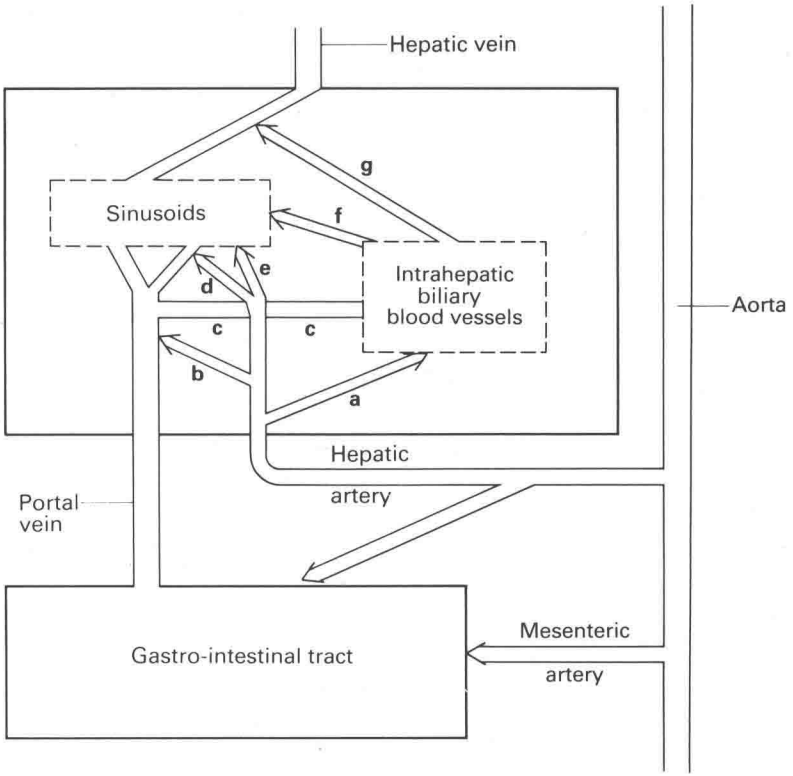

Fig. 1–6 Diagrammatic scheme of hepatic blood vessels. Branches from the hepatic artery are: a, to biliary vessels; b, anastomosis with small portal vein; c, the 'internal root'; d, junction with portal venous twig; e, to sinusoids; f, 'radicular portal vein' (Fig. 1–2b); g, translobular. In birds b, d and f have not been seen. g is not easily found in mammals but is common in penguins.

in acid. Although vascular casts are accurate and useful they do not show the relation of the vessels to cells. In a portal tract there is usually a single venous branch, except for the largest tracts in man and dog. Detailed studies do not appear to have been made on larger animals. The large veins do not supply sinusoids direct, but via short fine branches. After repeated branching, the vein becomes progressively smaller and terminal twigs of the vein flow into a kind of spray of large sinusoids. The small supply vessels, the inlet venules, run into large sinusoids and are frequently joined by a twig of the artery. In all species the *portal vein* has a muscular wall which is especially well-marked in the guinea pig. The shape of portal veins varies between different species and they taper more rapidly in the penguin than in the mammal. There are frequent

connections between the portal vein and veins of the biliary vessels, but only exceptionally are there anastomoses between portal veins of different tracts or between portal and hepatic veins.

The *hepatic artery* has no constant extrahepatic course, but in all mammals it anastomoses with surrounding arteries, so that ligation even near the hilum of the liver may not cut off all the arterial supply. Within the liver, branches of the hepatic artery run in the portal tracts, accompanying the portal vein and its branches. It supplies the bile duct and, in mammals, sends branches to small portal veins as well as to inlet supply venules. Some arterial twigs enter sinusoids. In frogs, well-defined arterial sinusoids probably exist. In penguins, the artery supplies the bile duct but no arteriovenous anastomoses have been seen and the portal vein and hepatic artery supply different sets of sinusoids. Although the pressure in the artery is much higher than that of the vein, connexions between them are not necessarily through capillaries and pulsation has been shown cinematographically in the inlet venule.

The *intrahepatic biliary vessels* are well-marked in mammals and birds, but have not been studied in other animals. They are more profuse near the hilum and the chief afferent supply is the hepatic artery. Veins run from them to the portal vein and are known as 'internal roots of the portal vein'. Another connexion of these vessels is to the sinusoids and is called 'the radicular root of the portal vein'. A third type of vein has been seen a few times in mammals but is common in penguins and runs from the biliary vessels to the hepatic vein, by-passing the parenchyma entirely. It has been named the translobular vein, and occurs in cirrhosis. (See Glossary.) The blood vessels of the gall bladder resemble those of the intrahepatic biliary ducts.

The *hepatic vein* of six species of mammal and three of birds studied by the author is very similar. The way in which it begins is best seen near the edge of the liver: several large sinusoids coalesce to form a central vein which then receives large sinusoids which look like bristles joining the core of a test-tube brush. Central veins join together and form sublobular veins, a term somewhat loosely applied to hepatic venous tributaries of moderate size. Although sinusoids still run into moderately large hepatic veins they are usually collected together to form a short vessel which is able to regulate the passage of blood into the hepatic venous tree – the small sluice of Deysach. The wall of the hepatic veins of dogs and related species contains a large amount of smooth muscle which can virtually prevent blood from leaving the liver. In spite of reports to the contrary, the hepatic veins of other species also contain smooth muscle, though in much smaller amounts than in the dog, and the author has seen considerable amounts in man. As yet, veins of birds have not been examined for smooth muscle.

1.5 Lymph and lymphatics

Normally the flow of lymph from almost all tissues depends upon the state of activity of the tissue. The composition is usually approximately that of plasma, excepting that there is very little protein present. Hepatic lymph is unique. The flow is at all times abundant, being of the order of 0.2 ml h^{-1} g^{-1} liver weight in dogs and rabbits, and there is nearly as much protein as in plasma. It is generally accepted that lymph is formed in the lobule where the endothelium is very permeable, but there are no lymphatics within the lobule and lymph, by definition, can exist only inside lymphatics. There are, however, many lymph vessels in portal tracts and strictly this is where lymph originates. Many workers believe that plasma passes through the pores of the endothelium into the perisinusoidal space. It then passes centrifugally, away from the hepatic vein to the boundary of the portal tracts where it enters lymph vessels. Once in the portal tracts lymph flows to the hilum and after emerging it passes to a node, or joins gut lymphatics, eventually draining into the cysterna magna, the main lymph vessel of the abdomen and thorax. A small amount of lymph usually drains alongside the hepatic vein, except in cats, again ending in the cysterna magna.

When blood pressure within the sinusoids is raised by disease, hypertrophy of hepatic lymphatics can result and there may be exudation of fluid, rich in protein, from the surface of the liver. It is difficult to explain why exudation should occur if lymph is formed from perisinusoidal fluid and the endothelium is as permeable as it is generally accepted, for one would expect the pressure to be approximately the same both sides of the capillary wall. Very few workers have considered this difficult point, and no explanation exists.

Some lymph appears to be formed in the portal tracts. Fluid is normally absorbed from the bile ducts and some probably enters lymph.

In summary, it appears that most hepatic lymph is derived from tissue fluid formed in the region of the hepatocytes and there is augmentation of this lymph from fluid formed in the portal tracts, some of which almost certainly comes from absorption from bile.

1.6 Nerves

Most of the hepatic nerves run to the liver alongside the hepatic artery. They enter the liver at the hilum and the majority of fibres run in the portal tracts, though some run with the hepatic vein. Although the nerves are profuse they are not readily seen in small tracts unless specially stained and are therefore not visible in Fig. 1–2a. Both sympathetic and parasympathetic systems supply the liver and they both contain efferent (motor) and afferent (sensory) fibres. The distribution and determination

of the fibres has not yet been settled: some workers describe fibres on hepatocytes while others consider the 'fibres' to be artefacts.

In mammals the sympathetic system to the liver arises in the lower thoracic and upper lumbar region of the spinal cord and there is some control from the higher centres of medulla and hypothalamus. Efferent fibres travel in the sympathetic chain and most synapse in either a ganglion or the coeliac plexus, though some synapses are almost certainly present in the liver itself. Most sympathetic efferent fibres are probably concerned with the control of blood vessels and glucose metabolism. The parasympathetic fibres may come direct from one or more of the main vagal abdominal tracts, or via the coeliac plexus. In man there is often a special branch of the vagus to the liver. This nerve is certainly motor to the gall bladder, causing it to contract after a meal, and may stimulate bile secretion.

The hepatic nerves have been very neglected, possibly because they are difficult to study and possibly because one can cut them without any great difference of function becoming apparent. But failure to react to section is not necessarily an indication that the nerves are unimportant.

About 50% of the fibres in the hepatic nerves are afferent. The purpose they serve is not really understood. There is great activity in the nerves of many species. Stimuli which are known to affect the frequency of afferent impulses coming from the liver are: (*a*) changes in pressure (i) in the bile duct, (ii) in the portal vein and (iii) in the hepatic vein; and (*b*) alteration of the sodium concentration, and of the colloidal osmotic pressure in perfusing fluid. Sensors of the concentration of glucose in blood have been demonstrated by indirect methods, and the evidence in their favour is strong. It has also been shown that stimulation of the hepatic nerves can alter blood pressure or, in the absence of any change of general blood pressure, the rate of blood flow in other abdominal organs. In other words, the liver can give rise to reflexes which can affect the rest of the body, but this fascinating field of study has been almost completely neglected.

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