CHAPTER 1

ANATOMICAL VARIATION OF LIVER AND ~~ITS~~ RELATIONSHIP WITH DIETARY PECULIARITIES OF BIRDS

The avian liver is large and bilobed with the right lobe usually ~~being~~ larger than the left ~~one~~. Its colour varies from light-brown to dark black-brown. Outer surfaces and margins seem to be smooth or wavy with other depressions representing the impressions of the other visceral organs that come in contact with its anterior surface (opposite to the surface facing towards abdomen).

The liver is relatively smaller in carnivores and graminivores, while it tends to be relatively large in piscivores and insectivores. In situ, liver has a convex and ~~an~~ uneven ventral surface that faces the abdominal wall. The liver is divided into two lobes by a deep caudal and a shallower cranial cleft known as the bridge. The craniodorsal part of the liver ~~is~~ extended ~~up~~ to the lungs. The other adjacent organs make typical impressions on liver, especially ~~on~~ its dorsal side. Thus the heart is accommodated in the cranial part of the parietal surface. The left lobe has the impressions of ~~a~~ gall bladder and muscular stomach on the visceral surface, while the right lobe ~~has~~ the impressions of the cranial parts of the duodenal loop with pancreas and the spleen in the medial part of the visceral surface. The impressions for the right testis can also be distinguished on the surface of the liver of the male birds (Martin, 1970). The vena cava passes through the cranial region of the right lobe. The hepatic veins and vena cava enter and leave respectively at the same sites. In the middle of the visceral surface, there is a groove, the fossa transeversa, through which two hepatic veins and two hepatic arteries enter with the two bile ducts leaving the liver through the same groove (Martin, 1970). From each lobe of the liver, the hepatic duct leads into the duodenum. Right hepatic duct may have a branch into the gall bladder or may be enlarged locally as a gall bladder, though its terminal part serve as cystic duct. The gall bladder is lacking in many avian species like Parakeet, Pigeon and Dove, a condition without any apparent phylogenic significance (Gorham and Ivy,1938). Gall bladder stores and concentrates the bile. The latter function is clearly demonstrated by Schmidt and Ivy (1937). Concentration of the bile is affected primarily by the amount of bile pigments and bile salts (Farner, 1941; Schmidt and Ivy, 1937). The concentration of buffering compounds is lower in gall bladder-bile than in the hepatic duct bile. The principal functions of bile in digestion are neutralization of the acidity of chyme and the emulsification of fats. The rate of bile secretion increases during feeding (Lavrenteva, 1963).

Its primary role in digestion is associated with the production of bile. Among its numerous non-digestive functions are the storage of lipids and glycogen, intricate interconversions associated with intermediary metabolism, synthesis of proteins and glycogen and the formation of uric acid. It also functions as a haematopoietic organ in embryonic and immediate post-embryonic periods (Sandreuter, 1951).

The Anatomical features of the two lobes of liver are similar, having either a single or double paranchymal lining known as simplex or duplex muralium respectively. Great variations with regard to size, shape and structure of the liver are found to occur in various birds that are known to differ in their diets. Histologically, liver is a continuous mass of paranchymal cells tunneled by capillaries that are lined by littoral cells known as Kupffer cells and which convey predominantly venous blood from gastrointestinal canal to heart. The walls known as muralium, are generally one cell thick in mammals and song birds (Elias, 1949) and two cell thick in lower vertebrates. Externally, the liver paranchyma is bound by a single layer of hepatic cells called external limiting cells (Elias, 1963), which is continuous with muralium of the internal limiting plates. The hepatic cells around the portal canal are named periportal limiting plates (Elias, 1949b). Since the limiting plates are continuous with the muralium everywhere in the liver, one may consider that the liver is constituted of a single plate of liver cells, extensively branched. These cells (composing the limiting plates) are slightly smaller, and stain darker than those of the internal portions of the muralium, probably because they receive blood supply from one side only (Elias, 1949b).

The structural arrangement of any organ is complementary to its function. The efficiency of liver in metabolic as well as secretory activities depends greatly on the cytoarchitecture of the organ. Though it is a well known fact that the function of liver is closely connected with the diet, details that correlate structure and the diet in birds are meagre.

In order to understand the anatomical and morphological variations of the liver in different groups of birds with differing diets, a comprehensive and comparative study on the anatomy and morphology of avian liver was conducted.

MATERIALS AND METHODS

The birds were shot from their natural habitat within the University Campus. They were immediately brought to the laboratory and after determining their weight, were disseeted to see the location of liver in situ. Several species of birds were thus collected and are listed groupwise in Table I. Grouping is done on the basis of their diets namely Carnivores, Insectivores, Omnivores and Graminivores.

Diagrams were drawn from the dissected specimens to show the locations and the relations of the liver to the other visceral organs in situ. The liver along with the gall bladder was immediately removed, blotted and weighed to obtain the liver to body weight ratio.

Anatomical as well as morphological studies of livers of birds were demonstrated by drawing the diagrams from different ~~sides~~ views like dorsal, ventral etc. The impressions made on it due to closely associated visceral organs which are generally on the dorsal side of the liver were also studied along with the length and breadth of the lobes. Volumes of the liver lobes, the shape and the size of liver and the bridge between the two lobes as well as the gall bladder were observed and recorded.

Small pieces of liver from each bird ~~studied~~ were fixed in Bouin's fixative for ~~the~~ histological studies. Routine methods ~~was~~ were employed for preparing paraffin sections and they were stained with haemotoxylin and eosin.

OBSERVATIONS

<u>GROUP I (Carnivores)</u> :(Figs. 1a & 2a)

In this group it was observed that both the right and left lobes of the livers of the birds were more or less similar in shape and size. Liver lobes had a smooth surface and their margins were thick and straight. As the birds in this group were larger in size, the liver was not compressed and the impressions for the visceral features showed one cell thickness of limiting plates i.e. simplex muralium (Figs. 4b, 5b, 6b & 8b).

<u>GROUP III (Omnivores)</u>: (Figs. 9a to 19a)

The liver ~~of~~ this group of birds ~~was~~ bilobed and the two lobes were unequal in length, the left ~~one reaching upto only~~ one third ~~of~~ the length of the right ~~one.~~ Margin of the lobes in these birds also was noticeably thin and wavy, though ~~lesser in degree to that seen amongst~~ Insectivores. The liver had impressions ~~for~~ different visceral organs, which were very well marked ~~like those observed~~ in insectivores. Bridge between the two lobes was not well marked but was broad and short and did not keep the two lobes well apart as seen in the case of carnivores. An interesting aspect observed in this group was the presence of a depression ~~on the dorsal side of their liver~~ where the testis ~~was found to fit in.~~ Ratio of body ~~weight~~ to liver weight was about 2.71. The gall bladder was elongated sac like structure. Simplex type of muralium was the histological feature (Figs. 10b,12b,15b,16b, 18b & 19b).

GROUP IV (Graminivores and Frugivores): (Figs.20a to 22a)

This group consists of Parakeet, Dove and Pigeon, differed from other groups in not having a gall bladder. In the case of Parakeet, both the liver lobes had smooth ventral surface and margin. The bridge which was quite big and broad, had an appearance similar to that observed in carnivores. Amongst the three members of the group studied, the Dove and Pigeon had comparatively smaller bridges between their liver lobes. The Pigeon had a more straighter margin than that of the Dove. The weight ratio of liver to the body was about 2.27 (Table I). The histological structure of livers of these birds was same as that of carnivores i.e. they were found to have a duplex muralium (Figs. 21b & 22b).

DISCUSSION

Structurally the liver is an organ that has undergone very little changes during the evolutionary history of vertebrates. This is a pointer to the significant role the liver plays in the physiology of vertebrates, because of which the organ has attained sufficient complexity and adaptibility very early in the evolutionary history of vertebrates. This fact becomes strikingly significant when we observe the tremendous stride the other organs like brain, kidney, heart and digestive tract, have taken to improve their structure and functions, culminating in obtaining the highest level of complexity in birds and mammals. Compared to these organs, the liver, in its turn has not undergone ~~much of~~ many structural and functional evolutionary changes as it had acquired the necessary adaptability sufficently early for what. In fact, the ability to perform a multitude of functions is due to the resistance of the liver in discarding, to a certain extent, its functional totipotentiality, thereby escaping the possibility of over specialization. The fact that the liver is still composed of not very specialized cells, can be seen from its ability to regenerate even after being divested of 90% of its total mass. Ref Being so constituted, the liver can exhibit amazing adaptability with regards to its size, shape, mass, microanatomy and functions according to the demand placed on it. Ref. Since, the main functions of the liver are correlated with the food and metabolism, it is not surprising that major adaptations of the liver are biochemical and linked with the diet.

must be - they perform 100's of very special jobs! ? Contradiction

From the data collected from the comparative study on the gross and micro-anatomy of liver of adult birds with different dietary preferences, it could be realized that dietary specialization have some correlations with these aspects of the liver. The liver weight:body weight ratio is lowest (1.8) in Carnivores and highest in Insectivores (3.0). This generally denotes that though the Carnivores are bigger in size, the liver is smaller as compared to their body, while the Insectivores, though smaller in size, have a greater liver mass. Such relationship of the liver to body weight has drawn the attention of many workers in the past. According to Magnan (1910) the liver is relatively smaller in carnivores and graminivores and larger in piscivores and insectivores. Magnan (1910) further stated that the Ducks fed on fish diet had much larger liver than those fed on grains or meat. In the light of these observations, one would be tempted to state that a protein rich food (of carnivores) or carbohydrate rich food (of frugivores and graminivores) alone does not increase the liver weight ratio, but a combination of protein and fat rich food,(when diet consists of fish or insects) can increase it. In other words, a mixed diet always influences the liver to attain larger dimensions in size and weight. Diets consisting of protein and carbohydrate, (as in the case of omnivores which consume both insects and grains) also have ~~has~~ the same effect on ~~their~~ liver where the ratio is very high (2.71).

In birds, a higher liver weight:body weight ratio poses a problem of ~~as to the~~ accommodation of the organ in the limited space in their visceral cavity. In insectivores, the liver solves this problem by becoming thin and elongated thereby occupying the available niches in the body cavity. Such cramping, inevitably leads to the development of impressions of the other visceral organs on the surface of the liver. On the other hand, in carnivores having a larger space in the body cavity, the liver is thick, massive and compact. The same reason i.e. the stringent availability of space, can also be given to the morphological differences of lobe the right and left lobes. In insectivores, the left is ~~shorter than the right one; left lobe is~~ only half the size of the right. In graminivores, the left lobe ~~one~~ is approximately two third of the right ~~lobe~~. In the birds of prey, with greater space available to the liver, both the ~~its~~ lobes attain equal size. The omnivores show an intermediate condition as to the size relationships of both lobes ~~left lobe to the right lobe~~.

The present observations on the liver weight : body weight ratio indicate a lower value for carnivores and higher value for insectivores, with intermediate values for omnivores and graminivores. From this data it could be surmised that carnivores and graminivores are similar in having lower liver ratio values while insectivores and omnivores are similar with a higher liver ratio value. In other words stenophagous birds like carnivores and graminivores have lower liver weight ratio. These birds are stenophagous not only with respect to the diet but even with respect to the organic constitution of the diet. The carnivore diet consists mainly of proteins while that of graminivores predominantly of carbohydrates. The euryphagous birds (omnivores) and insectivores (as well as piscivores as mentioned by Magnan, 1910) are found to have a larger liver weight ratio. Omnivores, by eating both insects and grains, consume both proteins and carbohydrates and can be said to be euryphagous with respect to organic dietary constituents too. In this latter context insectivores can also be regarded as euryphagous as the insect food (like a diet of fish) brings in both proteins and fat.

The relationship of liver in its structural design and mass to the stenophagous and euryphagous natures is further exemplified in microanatomical complexities too. It is interesting to note that carnivores and graminivores display a closeness by having a duplex muralium, while insectivores and omnivores depict propiquity by having a simplex muralium. At this juncture one can not avoid the consideration of the disclosures of Hans Elias (1963) that the simplex muralium is the more advanced and is found in mammals and song birds (Passerines) and the duplex is the earlier model found mostly in lower vertebrates. Further, Hickey and Elias (1954) working on 20 species of birds belonging to 5 different orders concluded that the passerines are the most highly evolved group of birds, having simplex type of muralium. In the light of these reports and present observations, it could be surmised that carnivores and graminivores with duplex muralium and lesser liver weight:body weight ratio are the earliest to evolve than the insectivores and omnivores that show simplex muralium and higher liver weight ratio. This could as well mean that stenophagy is more primitive than euryphagy. One is tempted to degress and state that euryphagy could be one of the reasons that culminated in the pre-emptive diversification of hominids from other basic primate groups which are still stenophagous.

The structural arrangement of liver cords into simplex or duplex types may have a synergistic influence on other structural and functional characteristics of the liver as well ~~too~~. The liver with the single muralium or liver plates will have larger sinusoids; increased blood flow due to less vascular resistance, and will have greater cellular surface areas that will come in contact with the fluid thereby establishing an intimate rapport between extracellular fluid and the intracellular cytoplasmic compartments. This will enhance the efficiency of the hepatic cells to respond to even minute changes in the circulating blood in the sinusoids. This increases the adaptability of the liver and thereby the adaptability of the birds themselves to consume any type of diet. Such functional adaptations of the liver with regards to food become more obvious in ~~are more revealed from~~ the studies (accompanying chapters) on the distribution pattern of several enzymes and metabolites.

TABLE I

Grouping of birds according to their dietary specializations

GROUP I - CARNIVORES	
1. Vulture (*Gyps bengalensis*)	Order: Falconiformes
2. Kite (*Milvus migrans*)	"
GROUP II - INSECTIVORES	
3. Cattle Egret (*Bubulcus ibis*)	Order: Ciconiformes
4. House Swift (*Apus affinis*)	Order: Apodiformes
5. Bee-Eater (*Merops orientalis*)	Order: Coraciformes
6. Tailor Bird (*Orthotomus sutorius*)	Order: Passeriformes
7. Martin (*Hirundo concolor*)	Order: Passeriformes
8. Drongo (*Dicrurus adsimilis*)	"
GROUP III - OMNIVORES	
9. Brahminy Myna (*Sturnus pagodarum*)	Order: Passeriformes
10. Common Myna (*Acridotheres tristis*)	"
11. Jungle Babbler (*Turdoides striatus*)	"
12. Indian Robin (*Saxicoloides fulicato*)	"
13. Bulbul (*Pycnonotus cafer*)	"
14. Koel (*Endynamys scolopacea*)	"
15. House Crow (*Corvus splendens*)	"
16. House Sparrow (*Passer domesticus*)	"
17. Barbet (*Megalaima haemacephala*)	Order: Piciformes
18. Fowl (*Gallus domesticus*)	Order: Galliformes
19. Duck (*Anas domesticus*)	Order: Anseriformes
GROUP IV - FRUGIVORES AND GRAMINIVORES	
20. Parakeet (*Psittaculus krameri*)	Order: Psittaciformes
21. Little Brown Dove (*Streptopelia senegalensis*)	Order: Columbiformes
22. Blue Rock Pigeon (*Columba livia*)	"

TABLE II

Body and liver weights and length of each lobe of the liver and liver weight : body weight ratio of representative birds of various dietary groups.

GROUP	BIRDS	BODY WT. (g)	LIVER WT. (g)	LENGTH Left (cm)	LENGTH Right (cm)	RATIO
GROUP I (CARNIVORES)						
1.	Vulture	4950	88.0	8.0	8.0	1.79
2.	Kite	740	14.2	4.5	3.5	1.91
GROUP II (INSECTIVORES)						
3.	Cattle Egret	360	10.8	4.2	4.1	2.98
4.	House Swift	23	0.8	3.7	1.9	3.47
5.	Bee-Eater	17	0.5	2.2	1.1	3.13
6.	Tailor Bird	8	0.2	2.1	1.5	3.31
7.	Martin	11	0.3	2.1	1.1	3.09
8.	Drongo	40	0.8	2.5	1.9	3.28
GROUP III (OMNIVORES)						
9.	Brahminy Myna	54	1.5	3.5	2.4	2.81
10.	Common Myna	120	3.2	5.4	2.7	2.68
11.	Babbler	70	1.5	3.4	2.3	2.24
12.	Indian Robin	20	0.4	3.0	1.4	2.22
13.	Bulbul	34	0.8	2.5	1.4	2.35
14.	Koel	220	8.1	4.6	2.8	3.63
15.	House Crow	195	5.5	5.4	3.5	2.82
16.	House Sparrow	25	0.9	3.0	1.5	3.63
17.	Barbet	37	0.7	2.3	1.2	2.36
18.	Fowl	1280	31.0	9.0	7.5	2.42
19.	Duck	1010	18.9	8.9	7.3	1.87
GROUP IV (FRUGIVORES & GRAMINIVORES)						
20.	Parakeet	115	2.4	3.4	2.2	2.09
21.	Little Brown Dove	111	2.3	4.1	2.1	2.07
22.	Pigeon	340	8.9	6.0	3.1	2.62

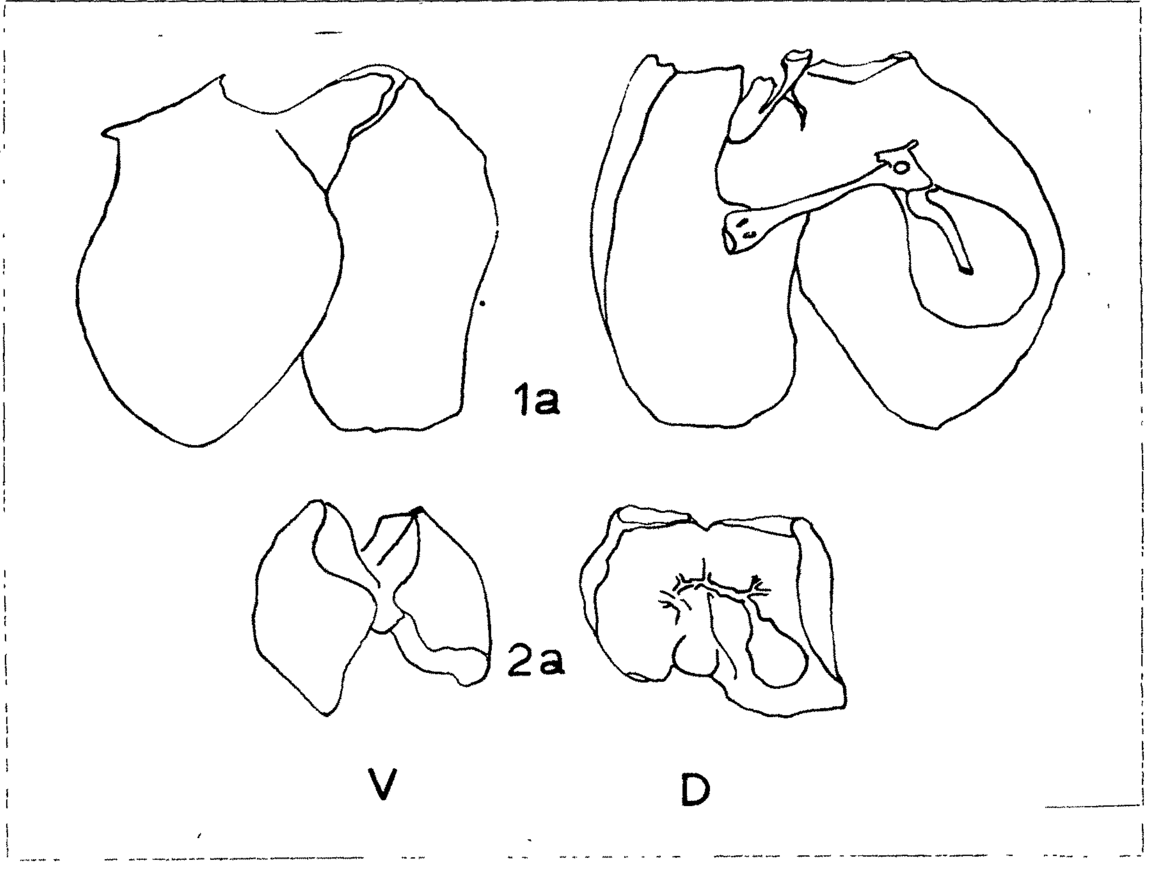
All are average values from five birds.

EXPLANATION TO FIGURES (CHAPTER 1)

Figs. 1a to 22a. Diagrams of anatomical features of livers of birds

Figs. 1b,4b,5b,6b,8b,10b,12b,15b,16b,18b,19b,21b,and 22b - Photomicrographs of liver of birds showing histological features - Haematoxylin-Eosin. All are magnified 200X.

Figs. 1a & b	Vulture
Fig. 2a	Kite
Figs. 4a & b	House Swift
Figs. 5a & b	Bee-Eater
Figs. 6a & b	Tailor Bird
Fig. 7a	Martin
Fig. 8a & b	Drongo
Fig. 9a	Brahminy Myna
Figs. 10a & b	Common Myna
Fig. 11a	Jungle Babbler
Figs. 12a & b	Indian Robin
Fig. 13a	Bulbul
Fig. 14a	Koel
Figs. 15a & b	House Crow
Figs. 16a & b	House Sparrow
Figs. 18a & b	Fowl
Figs. 19a & b	Duck
Fig. 20a	Parakeet
Figs. 21a & b	Dove
Figs. 22a & b	Pigeon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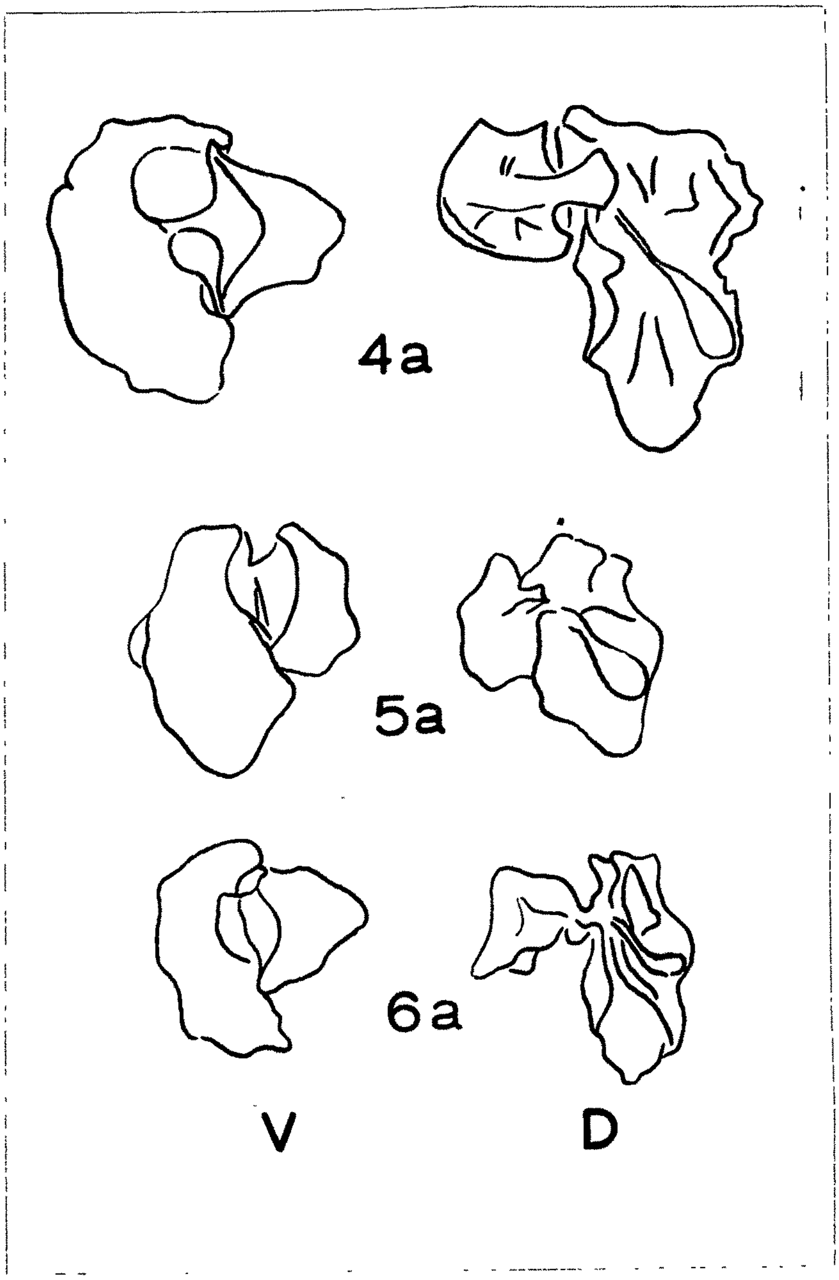
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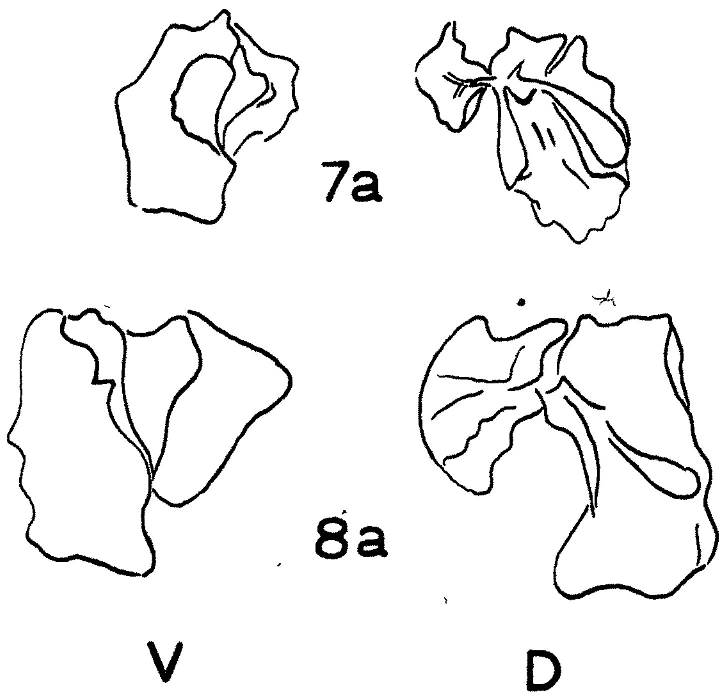
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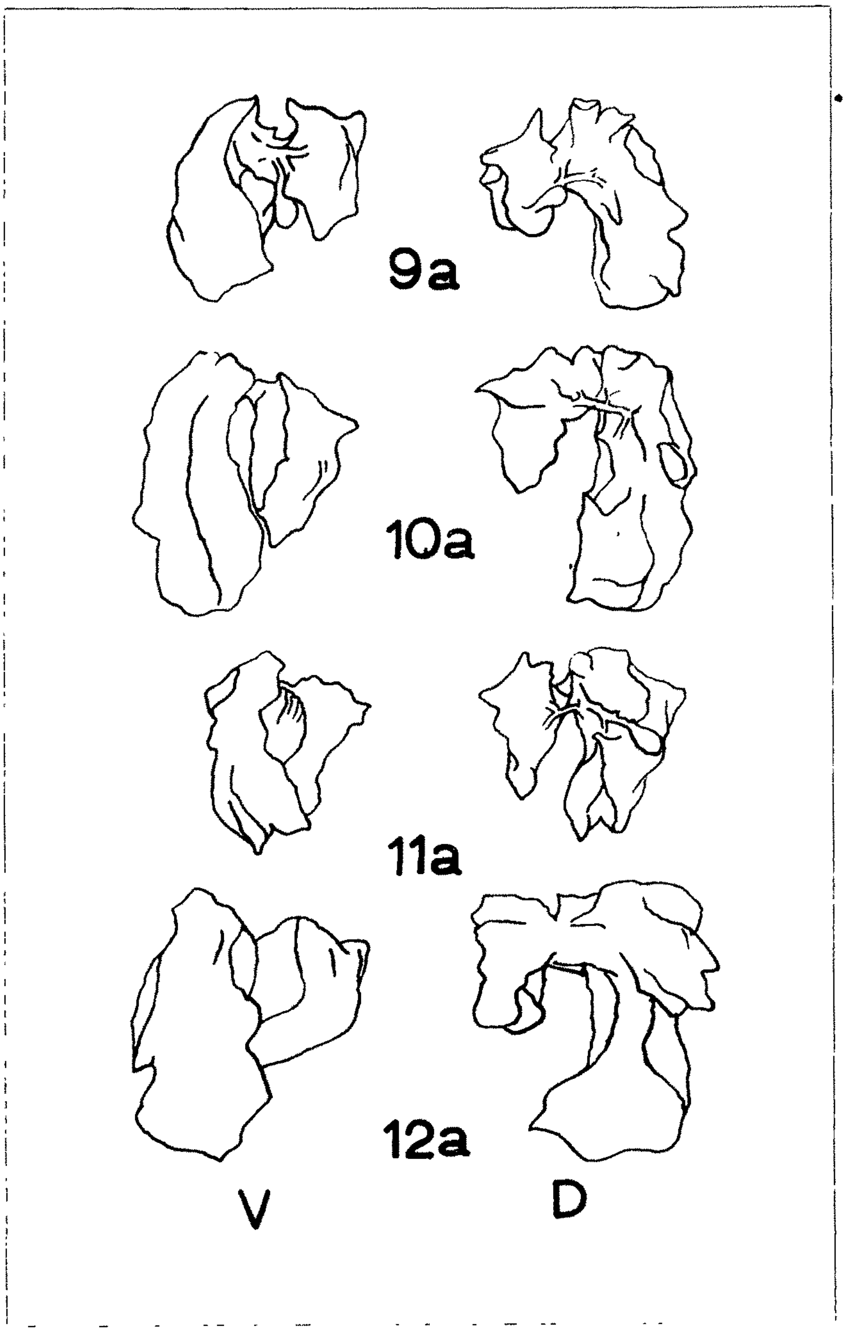
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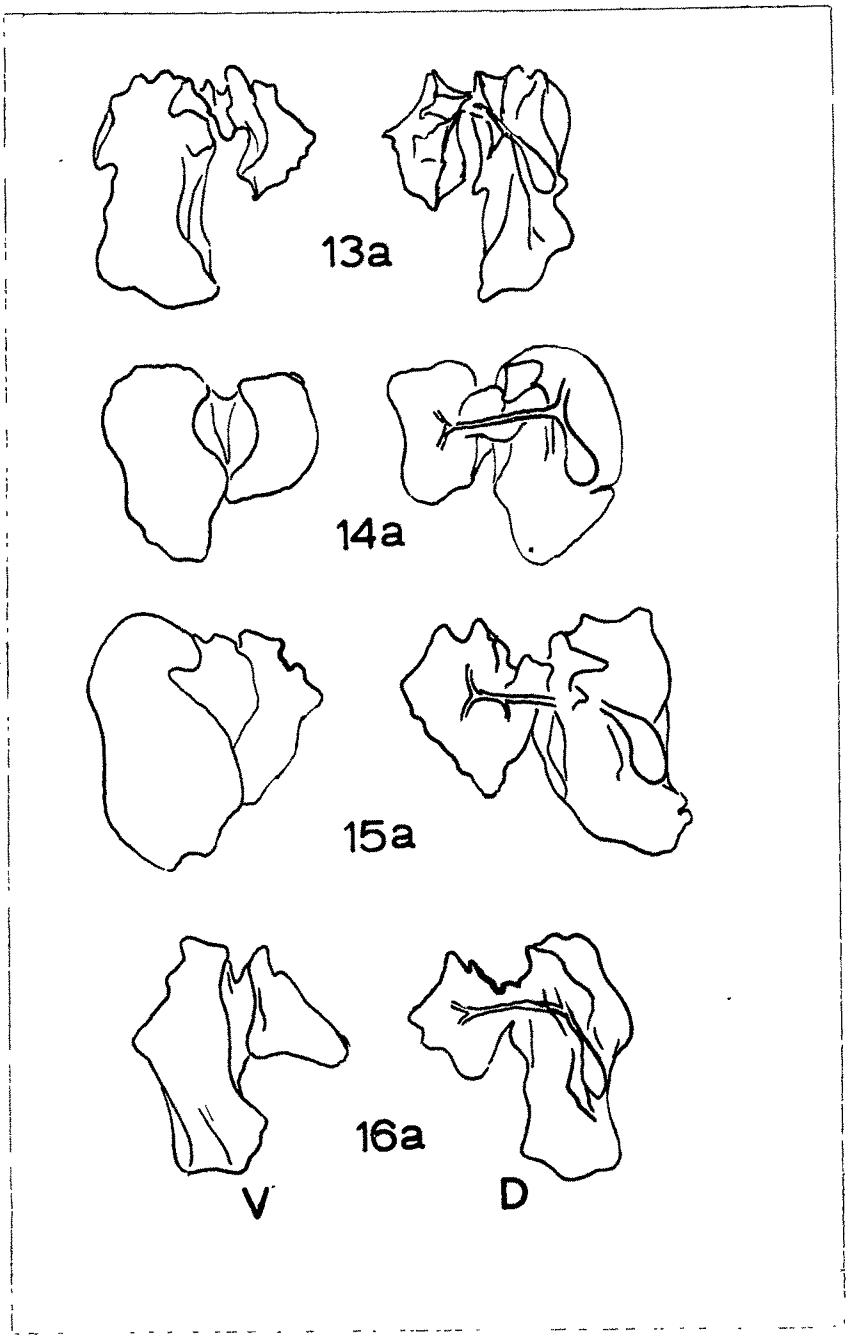
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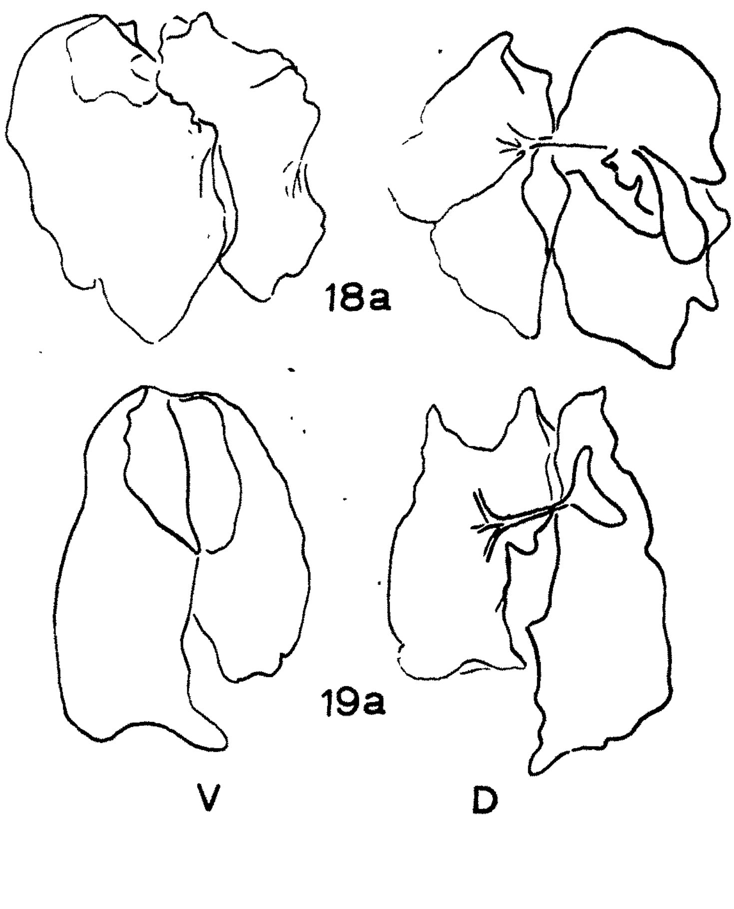
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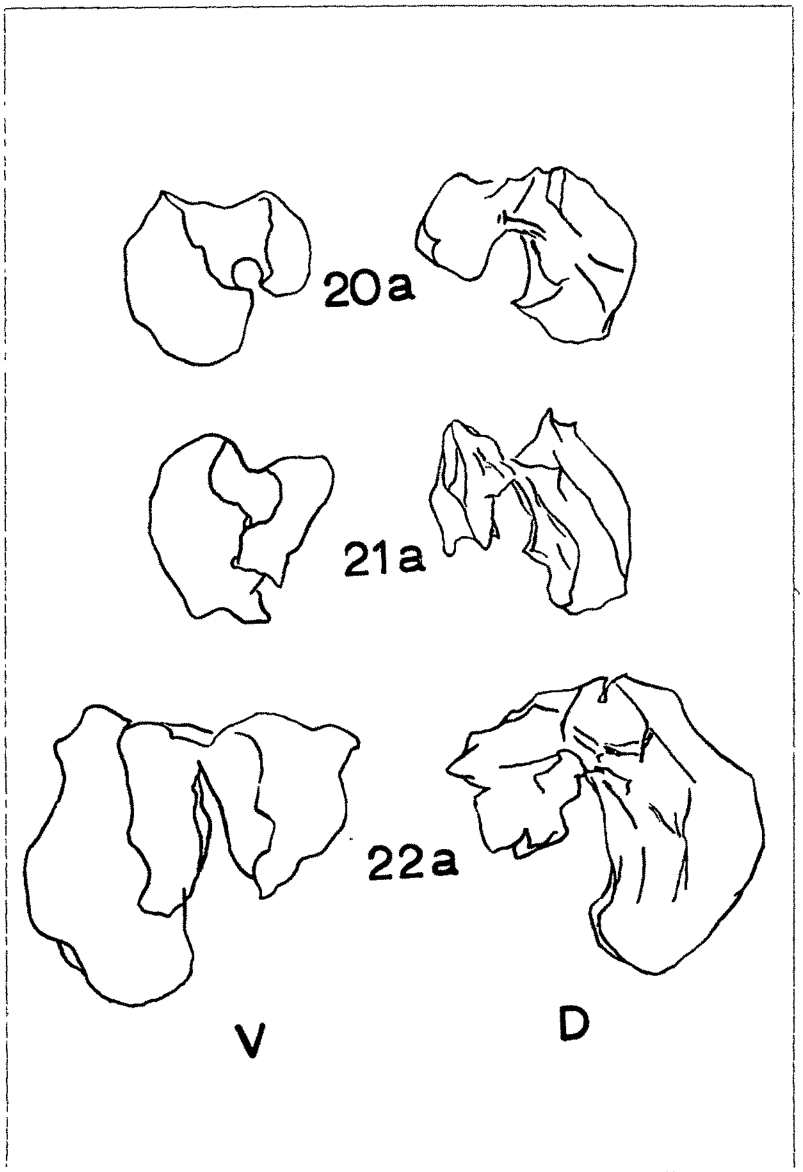
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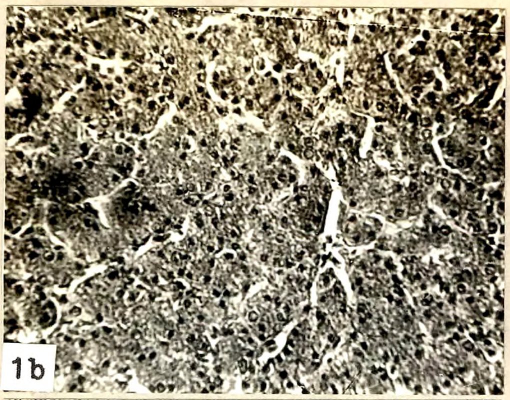
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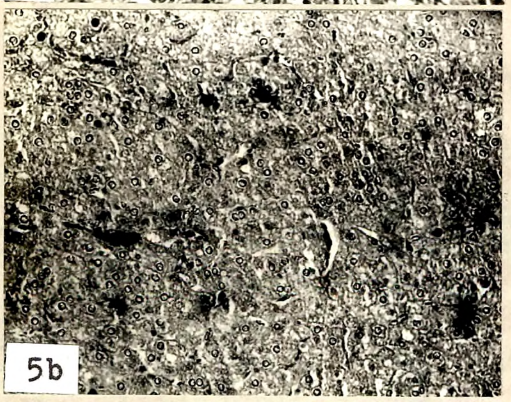
4b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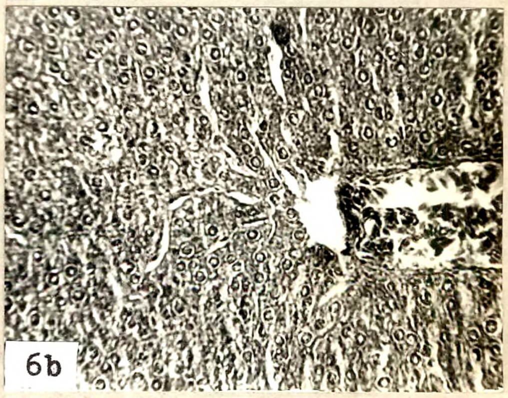
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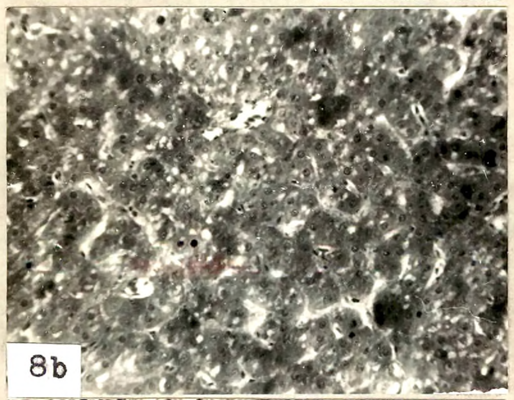
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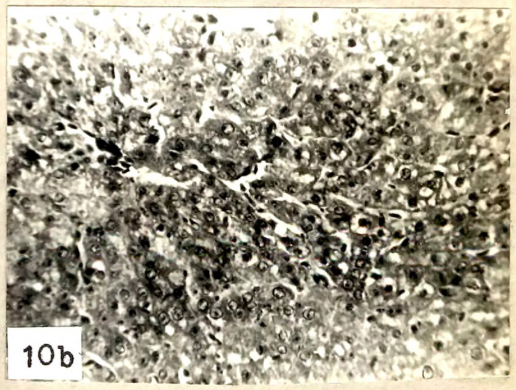
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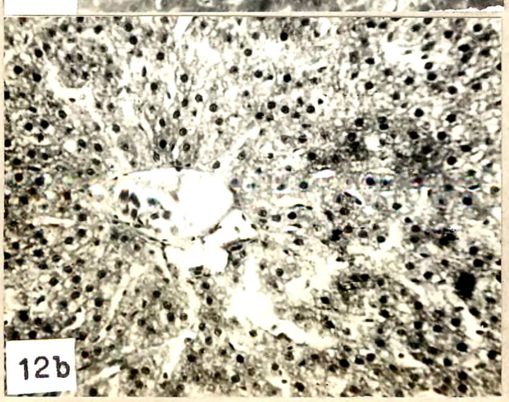
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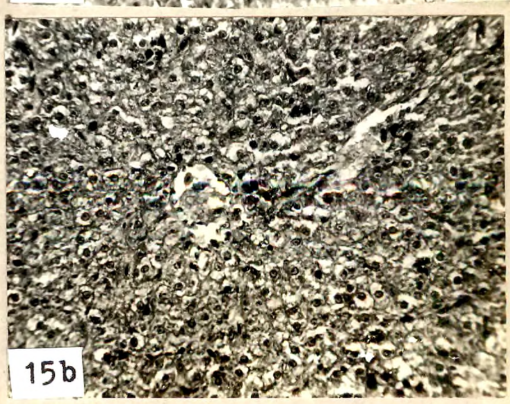
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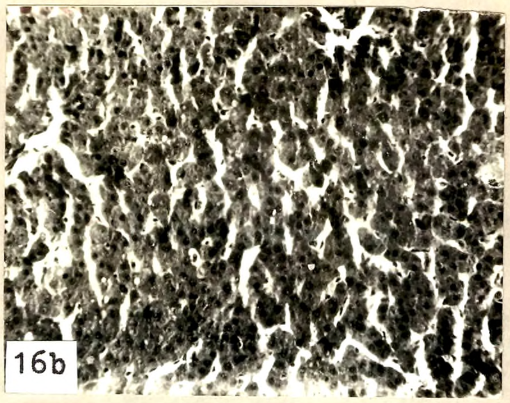

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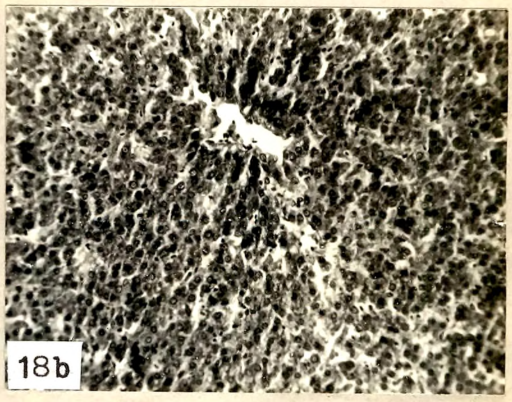

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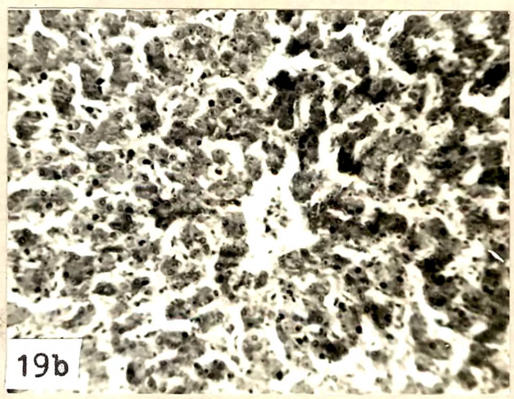

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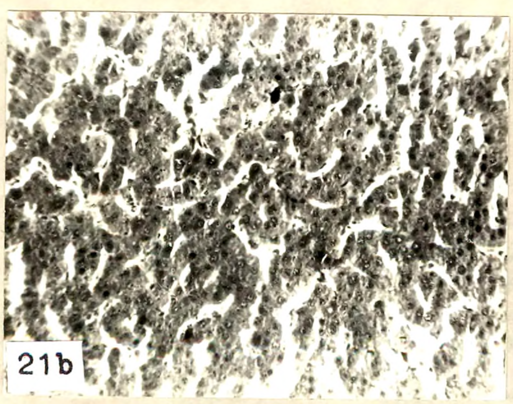

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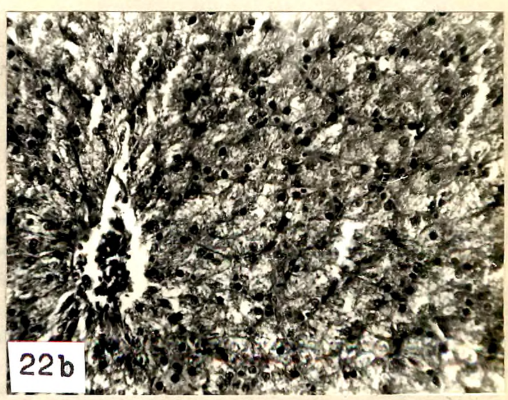

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