# THE STRUCTURE OF THE LIVER OF BIRDS

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THIS report is a preliminary study of the liver structure of birds. In it, 14 families were sampled. In a few previous papers, it was shown that the liver of vertebrates in general (except that in the later developmental stages of the Petromyzonidae) is a continuous mass of cells, tunneled by the lacunae hepatis in which the sinusoids are suspended (Elias, 1948; 1949a and 1949b; and Elias and Bengelsdorf, 1951 and 1952). The partitions (laminae hepatis, liver plates) between the lacunae are predominantly two-cells thick in Myxinidae, young Petromyzonidae, Selachii, Osteichthyes, Dipnoi, and Reptilia. Among the Amphibians there is a mixture of liver plates of one- and two-cell thickness within the same organ. In the Mammalia, however (that is, in all forms studied: including representatives of the Monotremata, Marsupialia, Rodentia, Artiodactyla, Perissodactyla, Carnivora, and Primates), the liver plates are always one cell thick. It has been shown that this specific mammalian liver structure provides a more stable construction from a mechanical viewpoint and that it also provides for greater physiological efficiency by increase of cell-blood contact surface and by increase of biliary outlet surface (Elias, 1952). In the same paper, the tentative suggestion was made that the change to liver walls of one-cell thickness was an important, if not indispensable, factor that allowed the rise of the mammals. This organ thus structurally improved, it was suggested, is more adequate for animals of higher metabolism and greater activity than the liver with two-cell-thick walls such as found in the lower vertebrates. In order to test this hypothesis, it became necessary to investigate the liver of the other homoeothermic class of vertebrates, namely that of the birds.

Among the vertebrates previously investigated (Elias and Bengelsdorf, 1952) there were two birds, the domestic chicken (*Gallus gallus*) showing plates of two-cell thickness and the Eastern Meadowlark (*Sturnella magna*) having uniformly one-cell-thick plates. The existence of two different kinds of liver structure in one class of vertebrates made it necessary, in order to gain insight into the avian liver in general, to extend this study to the representatives of as many different avian families as was practical.

## MATERIAL AND METHODS

The material consisted of domesticated birds and trapped wild birds. The canaries (*Serinus canarius*) were supplied by Mrs. J. K.

Keizer, Mrs. Edna Becker, and Stanley Saternus of The Greater Chicago Cage and Bird Club and the germ-free chickens by James A. Reyniers of the Lobund Laboratory of the University of Notre Dame. Of the wild birds, the ducks were furnished by Frank C. Bellrose, Jr. of the Illinois Natural History Survey; the House Sparrows (*Passer domesticus*) by Karl E. Bartel of the Inland Bird Banding Association; the others largely by Robert W. Nero of the University of Wisconsin. The livers were preserved by injecting 4 per cent formaldehyde solution into the liver, either through the portal vein or the upper part of the vena cava caudalis in large birds, or by injecting the fluid directly into the body of the liver. In both kinds of procedure, most of the blood is washed out of the sinusoids by the advancing fixing fluid, and the sinusoids are distended, therewith facilitating the histological analysis of the parenchyma. Serial sections of 8 microns thickness were prepared from all specimens, but recourse to reconstruction was not made, since in the previous publications by Elias and Bengelsdorf (1951 and 1952) criteria were established by which to judge the liver structure in single sections. Long, unending rows of cells, recurrent into themselves, seen in microtome sections indicate, as was explained previously, the existence (in the three-dimensional specimen from which the section was cut) of a continuous wall work. This rule was verified in all specimens examined. The introduction of a second criterion is necessary to determine the "histological" thickness of the liver plates. By histological thickness is meant the number of cell layers constituting a wall of these plates. This criterion will be described below.

## OBSERVATIONS

Plate 33 shows typical examples of the two types of livers found among birds. It is obvious from the plate that the Lapland Longspur (*Calcarius lapponicus*) possesses liver plates that are one-cell thick; but if we look at the liver of the Wood Duck (*Aix sponsa*), it is not immediately possible to decide whether the rows of cells which are two and more cells wide are normal sections of plates two or more cells thick or whether they are tangential sections of curved plates one cell thick. There are two methods by which this question can be decided without recourse to reconstruction, namely:

1. If a band-like area of liver parenchyma shows two rows of nuclei and if these nuclei are located in the middle of their respective cells, it is impossible to judge whether this particular band is a tangential or an oblique section of a plate one cell thick or whether it is a normal section of a wall two cells thick; but if in the entire specimen only very

few bands can be found which are less than two cells thick, we can conclude that most liver plates of that animal are two cells thick.

2. If the nuclei of a two-cell-wide parenchymal band are located at that side of the cells which is in contact with the blood vessels, it can be stated conclusively that this particular liver wall is two cells thick; for we can then distinguish two definite layers of cells showing a clear polarity, with a basal (paravascular) pole and a distal (intralaminar) pole.

A liver consisting of plates one cell thick shows the vast majority of plates cut at such angles that bands onecell wide result.

By means of these criteria, the histological thickness of the liver plates of all the species under investigation was determined. Plate 33 showing typical examples of each type will suffice to illustrate this paper. The specific results are listed in table 1.

## DISCUSSION

In listing the orders of birds in an approximate sequence of evolutionary development (table 1), it should be stressed that the relative positions of many groups is still uncertain, and that a two-dimensional system of presentation has inherent limitations. As Mayr and Amadon (1951) point out, the Galliformes have been considered the most primitive order by one author (Portmann, 1938) and among the most primitive by another (Stresemann, 1927–34). More than one-half of the 8,600 species of birds in the world today are included in the order Passeriformes, and there is general agreement that this is the most highly developed order in the class Aves.

Although our sample is admittedly a small one, it is apparent even in this preliminary investigation that the more primitive orders and families of birds possess both types of liver structure. The passerine segment of the sample consistently displays liver plates of one-cell thickness. In this development of its liver structure, the class Aves thus is somewhat comparable to Amphibia in its possession of liver plates that are either one or two cells thick. It is further obvious that one-cell thickness is not indispensable to the attainment of a homoeothermic condition.

The presence of both types of plates in the relatively primitive Anatidae and Phasianidae studied by us appears to rule out the evolution of one-cell thickness in a phylogenetic sequence, at least in birds. For, had the evolution of liver structure among the birds proceeded in a uniform sequence together with other characters, one would expect to find liver plates two cells thick among more primitive birds like the grebes and liver plates one cell thick among higher

TABLE 1

THICKNESS OF LIVER PLATES IN BIRDS ARRANGED IN APPROXIMATE ORDER OF EVOLUTIONARY DEVELOPMENT

| *Order* / *Family* | *Species* — *Scientific name* | *Species* — *Vernacular name* | *Number of Specimens* | *Thickness of liver plate* |
|---|---|---|---|---|
| Colymbiformes | | | | |
| Colymbidae | *Colymbus grisegena* | Holboell's Grebe | 1 | 1 cell |
| Anseriformes | | | | |
| Anatidae | *Anas acuta* | Pintail Duck | 1 | 1 and 2 |
| | *Aix sponsa* | Wood Duck | 6 | 2 |
| Galliformes | | | | |
| Tetraonidae | *Bonasa umbellus* | Ruffed Grouse | 3 | 1 and 2 |
| | *Tympanuchus cupido* | Prairie Chicken | 1 | 1 |
| Phasianidae | *Gallus gallus* | Domestic Chicken | 4 | 2 |
| Gruiformes | | | | |
| Rallidae | *Fulica americana* | American Coot | 3 | 2 |
| Passeriformes | | | | |
| Alaudidae | *Eremophila alpestris* | Horned Lark | 1 | 1 |
| Troglodytidae | *Troglodytes aëdon* | House Wren | 1 | 1 |
| Mimidae | *Dumetella carolinensis* | Catbird | 1 | 1?* |
| Turdidae | *Sialia sialis* | Bluebird | 1 | 1 |
| Sturnidae | *Sturnus vulgaris* | European Starling | 2 | 1 |
| Vireonidae | *Vireo olivaceus* | Red-eyed Vireo | 1 | 1 |
| Ploceidae | *Passer domesticus* | House Sparrow | 11 | 1 |
| Icteridae | *Sturnella neglecta* | Western Meadowlark | 2 | 1 |
| | *Sturnella magna* | Eastern Meadowlark | 1 | 1 |
| | *Agelaius phoeniceus* | Red-wing | 1 | 1 |
| Fringillidae | *Junco hyemalis* | Slate-colored Junco | 1 | 1 |
| | *Spizella arborea* | Tree Sparrow | 1 | 1 |
| | *Calcarius lapponicus* | Lapland Longspur | 1 | 1 |
| | *Serinus canarius* | Canary | 8 | 1 |

* Specimen imperfectly preserved.

birds, like the Passerines. However, the most primitive bird we examined, Holboell's Grebe, has liver plates of one-cell thickness. Of the two specimens of the Pintail, one was found with walls of one-cell thickness and one with walls of two-cell thickness, while all of six Wood Ducks examined had two-cell-thick liver walls. Among the Galliformes, both types of livers are encountered: 3 specimens of the Ruffed Grouse have walls one cell thick and one specimen has walls two cells thick. The only Prairie Chicken examined had a liver consisting of plates one cell thick, while four domestic chickens had two-cell-thick liver walls. Then, 3 specimens of a bird considered to be phylogenetically more advanced, the American Coot, possessed the primitive type of liver. Only among the Passeriformes is there uniformity. Thus it is obvious that the histological thickness of liver plates among the more primitive orders of recent birds is not firmly established, but subject to specific and even to individual differences. The pressure of natural selection has produced a wide variation in the evolution of a complex of subtle characteristics that

have enabled birds to succeed in occupying a variety of ecological niches. The average heart rate in Mourning Doves (*Zenaidura macroura*) is about 135 per minute; in much smaller birds the average runs as high as 615 (Odum, 1945). The composition of muscle tissue (presence or absence of myoglobin, etc.) likewise reflects adaptiveness to environmental conditions. In with these and many other anatomical, physiological, and psychological characters, the thickness of liver plates has varied as birds evolved under the force of natural selection.

## SUMMARY AND CONCLUSIONS

In 20 species of birds belonging to 5 orders, the highly developed Passeriformes (perching birds) consistently exhibited liver plates of one-cell thickness; among more primitive orders, these plates were either one or two cells thick.

Within the class of Aves, no orderly phylogenetic development of the liver structure was apparent in the 14 families studied. Histological examination of 52 specimens of these birds indicated that one-cell thickness is not a prerequisite to the attainment of a homoeothermic condition.

## LITERATURE CITED

ELIAS, HANS. 1948. Revision der Struktur der Säugerleber. Anat. Anz., 96: 454–460.

ELIAS, HANS. 1949a. A re-examination of the structure of the mammalian liver. I. Parenchymal architecture. Amer. Journ. Anat., 84: 311–333.

ELIAS, HANS. 1949b. A re-examination of the structure of the mammalian liver. II. The hepatic lobule and its relation to the vascular and biliary systems. Amer. Journ. Anat., 85: 379–456.

ELIAS, HANS. 1952. The geometry of cell shape and the adaptive evolution of the liver. Journ. Morph., 91: 365-388.

ELIAS, HANS, AND HERBERT BENGELSDORF. 1951. Die Struktur der Leber der Wirbeltiere. Anat. Nachr., 1: 273–280.

ELIAS, HANS, AND HERBERT BENGELSDORF. 1952. The structure of the liver of vertebrates. Acta Anatomica, 14: 297–337.

MAYR, ERNST, AND DEAN AMADON. 1951. A classification of recent birds. Amer. Mus. Novitates No. 1496.

ODUM, EUGENE P. 1945. The heart rate of small birds. Science, 101 (no. 2615): 153–154.

PORTMANN, ADOLPH. 1938. Beiträge zur Kenntnis der postembryonaten. Entwicklung der Vögel. Rev. Suisse Zool., 45: 273–348.

STRESEMANN, ERWIN. 1927–34. Aves. *In:* Handbuch der Zoologie ed. by Willy Kükenthal and Thilo Krumbach. v. 7, 2nd half. 899 pp.

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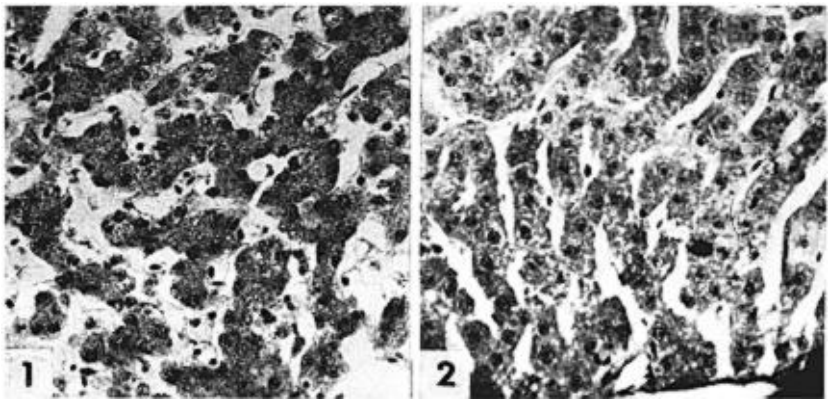


SECTIONS OF THE LIVER OF BIRDS. 8 microns, Hematoxylin and Eosin. (*1.*) Wood Duck. (*2.*) Lapland Longspur.