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JRE SURVEY ON GENERAL AND COMPARATIVE ENZYME BIOCHEMISTRY OF BIRDS

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Special Scientific Report—Wildlife No. 143

UNITED STATES DEPARTMENT OF THE INTERIOR
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LITERATURE SURVEY ON GENERAL AND COMPARATIVE ENZYME BIOCHEMISTRY OF BIRDS

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ABSTRACT

Available information on the enzyme biochemistry of birds is presented. A literature search revealed that birds differ mainly from other animals in metabolism involving nitrogen elimination. Comparative differences in enzyme biochemistry of only a few species of birds are known. Very little work has been done in the field of comparative enzyme biochemistry of birds, and practically none on blackbirds.

INTRODUCTION

Because information on the enzyme biochemistry, especially comparative enzyme biochemistry of birds, will be very helpful in basic studies of enzyme systems in nuisance birds, a survey was made of the available literature on enzymes, enzyme systems, and metabolism of domestic and wild birds, on general and comparative enzyme biochemistry, and on related techniques and procedures used in these studies.

This survey has relied heavily on the literature available in the libraries of the University of Florida, especially the Medical College Library. The libraries of the University of California at Berkeley and the University of Wisconsin at Madison also were visited. The Biological Sciences Library of the former and the Medical College Library of the latter were especially helpful. The survey was intended to cover all pertinent literature available, complete papers or abstracts, up to the spring of 1967.

The enzymes appearing in the literature are presented here in the six main classes as recommended in the Report of the Commission on Enzymes, International Union of Biochemistry (1965). The long-established trivial names of the enzymes are used because the systematic names recommended by the Commission are not yet in wide use. The six main classes of enzymes are given in the following order: 1. oxidoreductases, 2. transferases, 3. hydrolases, 4. lyases, 5. isomerases, and 6. ligases. Whenever feasible, the enzymes are presented in the numerical order of their respective Enzyme Classification Number and described under their source tissues. When more than one enzyme is mentioned in an article, the work is described only under one single enzyme as a matter of convenience; the rest of the enzymes are mentioned in their respective groups with reference to the described enzyme for details. The pertinent biochemistry is described with the enzymes. This survey also reports, under the title "Miscellaneous Enzymatic Reactions," those works in which some enzymatic reactions were mentioned but the enzyme or the enzyme systems were not specified. Finally, a table of the abbreviations used, and a table giving the trivial names of the enzymes surveyed, together with their recommended names and reactions, are contained in Appendices A and B, respectively.

ENZYMES SURVEYED

I. Enzymes Identified in Studies with Birds

1. Oxidoreductases

This class of enzymes catalyzes oxidation-reduction reactions. It includes dehydrogenases, oxidases, peroxidases, and oxygenases.

(1) Alcohol dehydrogenase

Eye tissue

The activities of alcohol dehydrogenase, lactate dehydrogenase, and malate dehydrogenase were found by Lukashevich (1964) to localize in the mitochondria of ellipsoids of the rods and cones of the retina of pigeons and other animals. In all the vertebrates studied the mitochondria of rods and cones located in the region of the ellipsoids showed a high endogenous dehydrogenase activity and high ADH, LDH, and MDH activities. Exposure of the retinas to light altered these activities in a manner that varied depending on the activity involved, the type of photoreceptor with which the mitochondria were associated, and the species of vertebrate. Because of the location of the enzymes and the fact that their activity was modified by the action of light, it was suggested that these three enzymes must participate in transmission of light stimuli from the outer to the inner part of photoreceptors.

Also see Chilson et al. (1966)—lactic dehydrogenase, p. 5.

(2) D-3-Phosphoglycerate dehydrogenase

Chicken liver

Willis and Sallach (1964) partially purified D-3-phosphoglycerate dehydrogenase from chicken liver and compared its distribution to D-glycerate dehydrogenase. They revealed a marked variation in the ratio of the activity of the first enzyme to that of the second enzyme among animals studied, and that birds had the highest levels of D-phosphoglycerate dehydrogenase. The enzyme was further purified by Walsh and Sallach (1965) and its properties determined. It was inhibited by N-ethylmaleimide, 3-bromopyruvate, and organic mercurials. Preincubation of the enzyme with NADH or NAD⁺, but not with phosphoglycerate, partially protected it against the first two reagents.

Also see Chilson et al. (1966)—lactic dehydrogenase, p. 5.

(3) Glucuronolactone reductase

Bulbul (Aves)

It is the absence of the microsomal enzymes (glucuronolactone reductase and uronolactonase) that prevents the successful synthesis of ascorbic acid in primates, ...and the bulbul (Reithel, 1967).

(4) Quinine dehydrogenase

Chicken kidney

The presence of oxidases of quinine in the chicken kidney, but not in the chicken liver, was reported. The enzymes in birds oxidized quinidine more rapidly than quinine, and the reverse was true for the enzyme of mammals (Berheim, 1952).

(5) Malic oxidase

Chicken blood

Hunter and Hunter (1957) in their comparative study of erythrocyte metabolism measured the oxygen consumption of whole cells and the activity of malic oxidase, succinoxidase, malic dehydrogenase, and lactic dehydrogenase of the homogenates of erythrocytes of chicken and other animals. They found that at a given temperature, the nucleated red blood cells of lower vertebrates, including birds, respire at a level considerably above that of the non-nucleated, mammalian erythrocytes. The succinoxidase activity of homogenates of chicken erythrocytes and the malic oxidase activity of homogenates of chicken, fish, and some sting rays are considerably higher than in other erythrocytes studied. The difference in activity cannot be correlated with the presence or absence of a nucleus.

Also see George and Talesara (1961c)—cytochrome oxidase, p. 14.

(6) Lactate dehydrogenase

a. Chicken heart, liver, and muscle

Wilson et al. (1963), compared the electrophoretic forms of starch gel, the (H) and (M) types, and the hybrid types of lactic dehydrogenase of the breast muscle of 38 species of wild birds and domestic duck and fowl with the pure (H) and (M) domestic fowl. Fondy et al. (1964), studied the comparative enzymology of lactic dehydrogenases, and isolated and crystallized the hybrid lactic dehydrogenases H₂M₂ from chicken liver and HM₂ from chicken leg muscle. The pure H₄ form of the enzyme had been isolated and crystallized from chicken liver and compared to the H₄ obtained from the heart. The fingerprint patterns of tryptic digests of the hybrids, the immunological properties, analog ratios, and oxalate inhibition were demonstrated. McKay and Kaplan (1964) determined the protein fluorescence polarization and the quantum yield of fluorescence per mold or tryptophan for the heart (H) and muscle (M) types of lactate dehydrogenases from chicken and beef. They found

that the (M) type had higher quantum yield than the (H) type. They also found increases in quantum yields of fluorescence on binding of NADH and the reduced 3-acetylpyridine analog of NADH for each of the enzymes. They suggested that the coenzymes might be bound closely to each other and might interact only with certain tryptophan residues in the enzyme. Pesce et al. (1964) reported methods for isolating and crystallizing in pure form the chicken and beef skeletal muscle (M) lactic dehydrogenase as well as chicken and beef heart (H) enzymes. They also characterized the enzymes. The four lactic dehydrogenases they isolated had somewhat similar amino acid compositions. Most striking differences had been found with the chicken muscle enzyme which contained approximately twice as many histidine residues as the other enzymes. The chicken muscle enzyme also contains significantly less glutamic acid and tyrosine. The phenylalanine content of the two (H) type enzymes is lower than that of the two (M) type enzymes. A greater difference in amino acid composition between the chicken heart and chicken muscle enzymes had been found than between the beef heart and beef muscle enzymes. The authors discussed the differences in properties of the enzymes with respect to the enzymes' evolutionary and structural significances.

Schapira and Dreyfus (1964) made a comparative study of lactic dehydrogenase isozymes of the skeletal muscle of the chicken. They found that there are marked differences between the embryonic and the adult muscle. In muscular atrophy and dystrophy the isozyme pattern resembles the embryonic pattern. The polymorphism of lactate dehydrogenase isozymes in wild, racing, and pure-bred pigeons was investigated by Zinkham et al. (1965). The isozyme patterns were found to be different.

The effects of temperature and substrate concentration on chick lactate dehydrogenase activity were investigated by Maisel and Kerrigan (1966). They showed by spectroanalysis that LDH in breast muscle supernatant and isolated LDH 5 had greater activity at high pyruvate concentration than at low. The difference was more marked at 40°C than at lower temperatures. Heart muscle LDH, and isolated LDH 1 reacted best at low pyruvate concentration. The difference was less marked at 40°C than at lower temperatures.

b. Chicken heart

Di Sabato and Kaplan (1964) studied the dissociation of lactic dehydrogenases from chicken heart and beef heart into subunits with sodium dodecyl sulfate. The dissociation of the enzymes into subunits was accompanied by a loss of enzymatic activity. They found that DPNH and its acetylpyridine analog protected the enzymes from dissociation. The coenzymes also protected

against loss of catalytic activity. Cahn (1964) reported that the lactate dehydrogenases isolated for chicken heart and from breast muscle differ markedly in kinetics, ability to react with coenzyme analogs, and electrophoretic mobilities. During embryonic development, the enzyme content of the breast muscle shifted from all heart type at early stages through intermediate enzyme levels and types to all muscle type shortly after hatching. Di Sabato (1965) showed that about 10 of the 30 tyrosyl residues of chicken heart lactic dehydrogenase were free to titrate between pH 8 and 11. He also showed evidence that the tyrosine residues of the enzyme form a part of the site binding of the coenzymes NAD. Fondy et al. (1965) made a further comparative study of lactic dehydrogenases isolated from 19 species. The sequence of the essential thiol peptide as isolated from chicken H₄ form of LDH was determined. This active site thiol peptide from the LDH's may be functionally related to the active site thiol region of the alcohol dehydrogenases.

c. Chicken embryo

Some cells in tissue culture and some tissues in chicken embryos were used in the study of the rate of synthesis of lactic dehydrogenase. It was found that it was regulated by the concentration of oxygen in the environment of the cells and the tissues. This was particularly true with the synthesis of the "muscle-type" of subunits of the enzyme (Goodfriend et al., 1966). Lindy and Rajasalmi (1966) showed that incubation of chick embryos in an hypoxic environment caused an increase in the proportion of tissue lactate dehydrogenase made up of subunit (H), whereas incubation in aerobic conditions decreased the proportional amount of subunit (M). The variation of ambient oxygen tension did not change the total lactate dehydrogenase activity. They believed that these results supported the hypothesis that oxygen or oxidative metabolites had an effect on the synthesis of the subunit peptides.

Chilson et al. (1966) investigated the dissociation properties and the reversible inactivation of chicken lactic and malic dehydrogenases. They found evidence for the existence of an intermediate form of lactic dehydrogenase with catalytic properties altered during reactivation. Comparison also was made with the dissociation properties of triosephosphate dehydrogenase, rabbit muscle α -glycerophosphate dehydrogenase, and horse liver alcohol dehydrogenase.

d. Gull nasal salt gland

McFarland et al. (1965) assayed the enzymes in the salt gland of adult western gulls. The average units of enzyme activity per gram of salt gland were as follows: lactic dehydrogenase,

90.1; phosphoglucomutase, 0.62; glucose-6-phosphate dehydrogenase, 1.40; aldolase, 2.86; isocitric dehydrogenase, 5.08; malic enzyme, 0.92; glutamic-oxaloacetic transaminase, 100.5; and glutamic-pyruvic transaminase, 0.50.

e. Chicken eye

Maisel et al. (1965) analyzed the ontogeny of LDH isozymes in the lens of the White Leghorn chick. They were able to show the progressive appearance of nine molecular forms.

f. Penguin

Stability of lactate dehydrogenase isozyme patterns in penguins was investigated by Markert and Sladen (1966). Three species were used. The starch-gel zymograms of penguins were found to be unusual in that the net charge on the isozymes is more positive than is true for mammals or other birds that have been investigated. In the adult, isozyme content of tissues were highly constant. The heart tissue pattern was the same as that of a fish. The zymograms prepared from various tissues of Merluccius bilinearis differed.

g. Peafowl

The multiple forms of lactate dehydrogenase of peafowl were studied by Rose and Wilson (1966). The electrophoretic properties of the peafowl isozymes were found to be unusual in that the isozyme from heart tissue can be either more or less anodic than that of muscle, depending on the pH.

Also see Lukashevich (1964)—alcohol dehydrogenase, p. 2;
Hunter and Hunter (1957)—malic oxidase, p. 3;
George and Talesara (1961c)—cytochrome oxidase, p. 14;
McDaniel and Chute (1961)—glutamic oxaloacetic
transaminase, Class 2, p. 18.

(7) Malic dehydrogenase

a. Chick embryo

Novikoff et al. (1948) showed the presence of DPN in the malic dehydrogenase system of early chick embryo.

b. Pigeon liver

Hsu and Lardy (1967a) prepared malate dehydrogenase from pigeon liver, purified it, and crystallized it as its triphosphopyridine nucleotide complex. The properties of the crystal were determined. The purified enzyme catalyzed the

decarboxylation of oxalacetate at a rate comparable to the decarboxylation of malate. Reversible inactivation of these activities occurred upon storage of the enzyme. Reactivation was obtained by incubation with dithiothreitol. They later studied (1967b) the fluorescence of the coenzyme binding of the purified enzyme, which fluoresced strongly with excitation and emission maxima at 293 and 350 m μ . Upon binding with TPNH, a blue shift in the emission maximum of TPNH from 465 to 440 m μ , accompanied by an enhancement of fluorescence intensity, takes place. The binding of the enzyme with L-malate or TPNH was specific, and was not observed with either D-malate or reduced diphosphopyridine nucleotide.

c. Chicken heart

Kitto and Kaplan (1966) isolated and purified the mitochondrial and supernatant forms of malic dehydrogenase from chicken heart. The supernatant and mitochondrial enzymes differed markedly in their amino acid composition and their peptide maps. Other comparative properties also were reported.

d. Enzyme evolution studies with malate dehydrogenase

Kitto and Wilson (1966) subjected heart extracts from over 100 species of birds to starch-gel electrophoresis. The "supernatant" form of malate dehydrogenase, which was present in every extract, was located on the gels. The mobility of this enzyme showed very little interspecific variation. Most birds tested had a supernatant malate dehydrogenase that moved as fast as the chicken enzyme. Hummingbirds and swifts, however, which were usually considered as two suborders of Apodiformes, were unique among the birds tested in having an enzyme that moved slower than the chicken enzyme. This finding appeared to confirm, they believed, the unity of the Apodiformes, an order whose unity had long been open to question. All families of the shorebird order (Charadriiformes) tested were unique in having an enzyme that moved at a definite distance from the chicken enzyme. The unity of this order of birds was also previously open to question.

Also see Lukashevich (1964)—alcohol dehydrogenase, p. 2;
Hunter and Hunter (1957)—malic oxidase, p. 3;
Chilson et al. (1966)—lactate dehydrogenase, p. 5;
McFarland et al. (1965)—lactate dehydrogenase, p. 5-6;
McDaniel and Chute (1961)—glutamic oxaloacetic
transaminase, Class 2, p. 18;
Rubinstein and Denstedt (1953)—citrate-cleavage
enzyme, Class 4, p. 34;
Goodridge and Ball (1966)—acetyl CoA carboxylase,
Class 6, p. 37-38.

(8) 6-Phosphategluconic dehydrogenase

Chicken blood

Salvidio et al. (1963) in their study of the glucose-6-phosphate and 6-phosphategluconic dehydrogenases activities in the red blood cells of several animal species, showed that 6-phosphategluconic dehydrogenase activity in pigeon red blood cells had an intermediate value of positivity, higher than that of human.

Also see Goodridge and Ball (1966)—acetyl CoA carboxylase, Class 6, p. 37-38.

(9) Glucose-6-phosphate dehydrogenase

a. Chick embryo

The glucose-6-phosphate dehydrogenase activity was found in the homogenates of chorioallantoic membranes of the chick embryo. This enzymatic activity recovered in the centrifugal supernatant fluid did not change appreciably with age of the embryo between 6 and 13 days (Kun, 1953). The activity of this enzyme in the developing chick embryo was found to localize primarily in skin and feather primordia of appendages from older embryo (Mahaffey, 1961).

b. Chick spinal cord

Burt and Wenger (1962) and Burt (1963) determined the activity of this enzyme in the spinal cord of the developing chick as an index of pentose cycle function during embryogenesis of the brachial chord. Their finding, they believed, supported the postulate that following cellular proliferation an early step in mural differentiation consisted of a transient rise in pentose cycle activity.

c. Chick embryo

Newburgh et al. (1962) used chick embryo explants in their study of the relation of enzymes glucose-6-phosphate dehydrogenase and isocitric dehydrogenase to protein and DNA accumulation. They found a much closer correlation of activities of the two enzymes with changes in DNA content than in the total protein content.

Also see McFarland et al. (1965)—lactate dehydrogenase, p. 5-6;
Goodridge and Ball (1966)—acetyl CoA carboxylase,
Class 6, p. 37-38.

(10) Triosephosphate dehydrogenases

Turkey breast muscle

Turkey and other animals were used in the study of the effect of tetrathionate on the stability and immunological properties of muscle triosephosphate dehydrogenases. When the three sulfhydryl groups of the enzymes were modified by tetrathionate, the enzymes were completely inhibited. Depending on the temperature and length of incubation with the inhibitor, this inhibition could be reversed by the addition of thiols. While the immunological properties of the inactivated turkey TPD differed significantly from the native enzyme, the immunological properties of the sturgeon enzyme were only slightly altered (Allison and Kaplan, 1964). A comparative study was made on the enzymology of triosephosphate dehydrogenases from chicken, pheasant, and turkey breast muscles, and those from the human breast, the skeletal muscle, and the tail muscle of lobster. Their physical, chemical, and immunological properties were compared with those of rabbit muscle and yeast (Allison, 1964).

Also see Chilson et al. (1966)—lactate dehydrogenase, p. 5;
Rinaudo (1962)—hexosephosphate isomerase, Class 5,
p. 36.

(11) Oestradiol-17 β -dehydrogenase

Chicken and pigeon blood

Portius and Repke (1960) demonstrated the presence of oestradiol-17 β -dehydrogenase in the blood of pigeon and hen and other vertebrates. However, sheep, goat, and cow contained oestradiol-17 α -dehydrogenase.

(12) Xanthine oxidase

a. Pigeon liver and kidney

Two tissues were necessary for uric acid synthesis in pigeon. The primary step, the binding of ammonia with some uncertain source of carbon, occurred in the liver where hypoxanthine was formed. The final conversion into uric acid, which took place in the kidney (or pancreas), was an oxidation catalyzed by xanthine oxidase (Edson et al., 1936). Goodwin (1960), however, reported that pigeon liver did not contain xanthine oxidase and thus did not oxidize to uric acid.

b. Chicken tissue

Croisille (1964) showed that hypoxanthine dehydrogenase (xanthine oxidase) was synthesized in different tissues at three very different periods during development of the chick.

The enzyme was almost specifically localized in the kidney during embryonic life; after hatching, it was present mainly in the liver. The enzymatic activity in the different tissues of the chick could be attributed to the presence of two very closely related proteins—one present in the mesonephros and the definitive kidney; the other present in the liver, the intestine, and the pancreas. The sites responsible for the antigenic and enzymatic properties of the molecule appeared to be different.

(13) Xanthine dehydrogenase

a. Chick liver

De Angelis and Totter (1964) studied the kinetics of hydrogen transfer between hypoxanthine and dimethylbiacridylium nitrate in the presence of chick liver xanthine dehydrogenase. They found that a two electron transfer from hypoxanthine to 10,10'-dimethyl-9,9'-biacridylium ions (DBA⁺⁺), followed by reoxidation of the reduced DBA⁺⁺ by oxygen, could account largely for the initial velocity of uric acid production catalyzed by chick liver xanthine dehydrogenase in the presence of DBA⁺⁺. The sensitivity of the chain reaction was discussed. Stirpe and Corte (1965) reported that xanthine dehydrogenase activity of chick liver increased during starvation. Administration of inosine, and possibly of adenine, had a comparable effect on the xanthine dehydrogenase, and also induced an elevation of the total quantity of enzyme. Hypoxanthine, xanthine, guanine, xanthosine, guanosine, and adenosine were ineffective. Cortisone was equally ineffective. The administration of puromycin abolished the effect of inosine and reduced that of starvation. Inosine induced increased synthesis of xanthine dehydrogenase, whereas during starvation the enzyme was spared with respect to other liver proteins. The authors suggested that chick liver xanthine dehydrogenase is an adaptive enzyme.

b. Chicken kidney

Cardona et al. (1965) studied in vitro the enzyme system xanthine dehydrogenase (XDH) in chicken tissue utilizing tissue homogenates, xanthine (sodium salt) as substrate, and methylene blue as hydrogen acceptor. Optimum conditions were determined for the enzymatic activity. Kinetic studies also were conducted with inhibitor and activators.

(14) Succinic dehydrogenase

a. Pigeon muscle

The relative quantitative distribution pattern of the narrow red and broad white fibers, and the succinic dehydrogenase

activity in the different layers of the pigeon breast muscle were studied quantitatively. The activity of this enzyme in any particular layer of the muscle was related to the number of the narrow red fibers present as the main bulk of the enzyme resided in these fibers (George and Talesara, 1960). This enzyme and cytochrome oxidase activity in pigeon muscle were studied by means of histological methods. Succinic dehydrogenase was detected in broad white fibers. The presence of a large number of succinoxidase-positive granules in the narrow red fibers accounted for their high oxidative metabolism. The presence of fewer, and smaller, succinoxidase-positive granules in the broad white fibers accounted for their smaller oxidative activity. The granules were suggested to be mitochondria (George and Talesara, 1961a). Later the study on succinic dehydrogenase included a few representative types of birds and a bat. In all the birds and the bat the pectoralis major muscle showed higher activity than the pectoralis minor, which indicated that of the two, the former muscle was metabolically much active and highly evolved. The pectoralis major muscle of the rosy parakeet, sparrow, bat, parakeet, and pigeon showed higher concentrations of succinic dehydrogenase as compared to the other birds studied whereas the fowl, a nonflier, showed the lowest enzyme concentration. In the birds studied a reciprocal relationship was found between the enzyme activity of the pectoralis major muscle and the body weight, fiber diameter, and weight of the pectoralis muscle (George and Talesara, 1961b).

Succinic dehydrogenase in pigeon pectoralis during disuse atrophy was investigated by Cherian et al. (1965). Muscle enzyme activity decreased from the first day, reaching its lowest level after 7 days. Histochemical observations on red and white muscle fibers showed that after 7 day's atrophy the majority of red fibers had lower enzyme activity; a few others showed higher activity. In white fibers, on the other hand, a uniform increase over normal in enzyme activity and mitochondrial number was noticed. These changes in the two types of fibers were less conspicuous during the later stages of atrophy. The authors suggested that in both red and white fibers there was a shift from aerobic to anaerobic metabolism, or vice versa. Histochemical study of oxidative enzymes showed that the striated muscle fibers of various kinds of vertebrate muscles fell into three types—small red muscle fibers which showed higher activities, large white fibers with lower activities, and "medium fibers" with intermediate activities. The chicken muscle was composed of three types of fibers, while pigeon and lovebird muscles displayed two types of fibers (Ogata and Mori, 1964).

b. Pigeon taste bud

Pevzner (1964) found succinic dehydrogenase activity to be localized in the taste buds of pigeon and other vertebrates. The author also observed that the localization and degree of enzymatic activity in mitochondria of the taste buds remained essentially constant for the animals on various steps of the evolutionary ladder.

c. Pigeon heart

Lee (1963) prepared pigeon heart mitochondria by sonication and also used digitonin to treat particles from pigeon heart. He found that the relative values of ATPase : NADH oxidase : succinate oxidase : energy-linked NAD reductase : energy-linked ferrocyclochrome c oxidase in $\mu\text{mole}/\text{min}/\text{mg}$ protein were 1180:470:31:40:2.4 for sonicated preparation and 230:190:14:5.5:12 for digitonin-treated particles.

d. Chicken embryo

Masai et al. (1965) localized the succinic dehydrogenase and monoamino oxidase activity in the central nervous system of the chick embryo by means of a histochemical method. They postulated that the neural tube was subdivided into columns.

Also see Hunter and Hunter (1957)—malic oxidase, p. 3;
George and Vallyathan (1964)—lipase, Class 3, p. 21;
Rubinstein and Denstedt (1953)—citrate-cleavage
enzyme, Class 4, p. 34.

(15) Glutamate dehydrogenase

Chicken and pigeon liver

Frieden (1965) isolated glutamate dehydrogenases from animal and nonanimal sources, and used the beef liver enzyme for comparison for effects of purine nucleotides on their properties. The enzymes from all animal sources were strongly and specifically affected by purine nucleotides. The binding constants and extent of activation or inhibition differed with different enzymes. However, the enzymes from pigeon and chicken livers appeared identical and they were different from those from mammalian livers.

(16) Folic acid reductase

Chicken liver

Folic acid reductase from chicken liver was used by Rothenberg (1965) to reduce the tritiated folic acid to tetrahydrofolic

acid with reduced triphosphopyridine nucleotide as the cofactor. From this he developed a method for determining methotrexate levels in biological fluids.

Also see Matsubara and Akino (1964)—sepiapterin reductase, p. 13.

(17) Dihydrofolic reductase

Chicken liver

Mathews and Huennekens (1963) highly purified dihydrofolic reductase from chicken liver. The enzyme was characterized, and its reaction reversibility demonstrated. Kaufman (1963) found that under a variety of conditions the activity of dihydrofolic reductase was stimulated in a qualitatively similar manner by salts, urea, formamide, and possibly hydrogen ions.

Also see Matsubara and Akino (1964)—sepiapterin reductase, p. 13.

(18) Sepiapterin reductase

Chicken liver

The presence of this enzyme in chicken was reported by Matsubara and Akino (1964).

(19) Cystine reductase

Chicken liver

Cazorla and Barron (1958) showed that the embryonic liver of chicken contained cystine reductase. The enzyme reduced cystine to cysteine with DPNH as the specific coenzyme. TPNH was ineffective. They also found that glutathione reductase, TPNH-specific, was also present.

(20) Uricase

Chicken embryo

Prosser and Brown (1961) in their description of uricolytic enzymes, stated that uricase activity in chick embryo increased up to 10 days only.

(21) Glutathione reductase

Chicken liver

The activity of the enzyme glutathione reductase was significantly lower in the liver preparations from vitamin B₁₂-deficient chicks than in those from normal chicks (Biswas and Johnson, 1964).

Also see Cazorla and Barron (1958)—cystine reductase, p. 13.

(22) Catalase

Chicken blood

Foulkes and Lemberg (1949-1950) presented the comparative amounts of catalase activities in these three species: horse, 1500; chicken, 86; and duck, 4.

Also see Cohen and Hochstein (1963)—glutathione peroxidase, p. 14.

(23) Cytochrome oxidase

Pigeon muscle

George and Talesara (1961c) quantitatively studied the distribution pattern of cytochrome oxidase, malic oxidase, succinoxidase, lactic dehydrogenase, and lipase in the different layers of pigeon breast muscle. The values derived for the individual red as well as white fibers indicated that the bulk of all the enzymes studied resided in the red fibers. These enzymes occur in only very low concentrations in the white fibers.

Also see Lee (1963)—succinate dehydrogenase, p. 12;
George and Talesara (1960)—succinate dehydrogenase, p. 10-11.

(24) Glutathione peroxidase

Duck blood

Catalase-deficient duck erythrocyte cells were protected against the toxic effects of low hydrogen peroxide concentrations by sustained glutathione peroxidase activity (Cohen and Hochstein, 1963).

(25) Cytochrome c reductase

See Lee (1963)—succinate dehydrogenase, p. 12.

(26) Monoamine oxidase

See Aprison et al. (1964)—hydroxytryptophan decarboxylase, Class 4, p. 34.

(27) Isocitric dehydrogenase

See McFarland et al. (1965)—lactate dehydrogenase, p. 5-6;
Newburgh et al. (1962)—glucose-6-phosphate dehydrogenase, p. 8;
Rubinstein and Denstedt (1953)—citrate-change enzyme, Class 4, p. 34.

(28) D-Glycerate dehydrogenase

See Willis and Sallach (1964)—D-3-phosphoglycerate dehydrogenase, p. 2.

(29) Tryptophan pyrrolase

See Knox and Eppenberger (1966)—tyrosine transaminase, Class 2, p. 18.

(30) β -Hydroxybutyrate dehydrogenase and

(31) Diaphorase

See Hellerström (1963)—alkaline and acid phosphatases, Class 3, p. 24.

2. Transferases

This group of enzymes catalyzes group transfer. It includes transaminases, kinases, and transacetylases.

(1) Catechol methyltransferase

Chick embryo

The actions of epinephrine on the innervated embryonic chick heart were terminated primarily through the metabolism by means of catechol-O-methyltransferase (McCarty and Shideman, 1960).

(2) Ornithine carbamyl transferase

Chicken tissues

Sirén (1963) studied the arginine metabolism in chicken. Arginine is an essential amino acid for birds. The author, in order to clarify whether chicken could synthesize arginine, determined the activity of ornithine carbamyl transferase, which is an enzyme in the urea cycle in different organs of the chicken. The enzyme was found to be absent, and no inhibitor was found. He concluded that chicken could not synthesize arginine.

(3) Carnitine acetyltransferase

Chicken breast muscle

Beenackers and Klingenberg (1963) showed that pigeon breast muscle had the highest activity of the enzyme carnitine acetyltransferase in mitochondria with acetylcarnitine as substrate of any animals tested. This enzymatic activity later was found also in pigeon breast muscle by Chase et al. (1965).

(4) Phosphorylase

Pigeon liver

The activity of phosphorylase in pigeon liver was higher as compared to that of glycogen synthetase. While G6P activated and UMP inhibited synthetase, G6P inhibited and UMP activated phosphorylase. 2-Deoxy-G6P acted in the same way to G6P (Fridland and Nigam, 1965).

(5) Glycogen phosphorylase

Chick embryo

Guha and Wegmann (1961) showed that ATP and Mg^{++} were needed in the histochemical demonstration of glycogen phosphorylase in the chick-embryo liver. Grillo (1961) further localized the enzyme in the liver parenchyma. It occurred in the liver parenchyma from the seventh day onwards, in cardiac muscle from the third day onwards, and in skeletal muscle from the 13th day onwards. The authors suggested that although phosphorylase was important in glycogenolysis it could not initiate the formation of glycogen in embryonic tissues.

(6) Uridine diphosphate glucose-glycogen synthetase

Chick embryo

Grillo and Ozone (1962) assayed UDPG-synthetase activities in chick-embryo tissues. In heart, liver, skeletal muscle, and brain, UDPG activities occurred earlier in development than phosphorylase and paralleled the appearance of glycogen in tissues. Glycogen synthesis occurred without insulin.

(7) Glutamine phosphoribosyl-pyrophosphate amidotransferase

a. Pigeon liver

Caskey et al. (1964) purified the enzyme from pigeon liver, and conducted inhibition studies. They concluded that the enzyme was susceptible to inhibitors only when in a specific conformational state, and that inhibitors acted by distorting the enzyme and reducing its activity.

b. Chicken liver

Hartman (1963a, 1963b) purified the enzyme from chicken liver, and made it apparently homogenous in the ultracentrifuge. It was inhibited by an analog of glutamine, and it had 10 iron atoms per molecule. Chelation of the iron atoms inhibited the enzymatic activity.

(8) Glucokinase

Pigeon muscle

Marcus and Manery (1966) studied the potassium stimulation of oxidation and phosphorylation in pigeon-muscle mitochondria. They used α -ketoglutarate as substrate and hexokinase—glucose phosphate acceptor system. It was found that the rate of phosphorylation was stimulated to an even greater extent than the rate of oxidation as sodium was replaced by potassium. In every preparation tested, the rates of phosphorylation and the P/O ratios were higher in the high-potassium media than in the high-sodium media.

(9) NAD kinase

Pigeon liver

Nemchinskaya (1963) found an enzymatic system for NADP synthesis from NAD and ATP in hyaloplasm of pigeon liver cells. The NAD kinase was stable during initial purification for 1 month.

(10) Creatine kinase

Chicken brain, heart, and muscle

Dawson et al. (1965) showed that in chicken all muscle contained only one creatine kinase, "muscle enzyme". Brain contained exclusively "brain enzyme". Yeast contained "brain enzyme" and might contain the intermediate enzyme. They showed that creatine kinase was an enzyme whose structure was that of a dimer.

Eppenberger et al. (1967) and Dawson et al. (1967) studied the comparative enzymology of creatine kinases. They purified two creatine kinases from chicken brain and muscle and compared them to those from the rabbit. There were significant differences in amino acid composition between the brain and muscle types; the hybrid enzyme had an intermediate composition. Antibodies prepared against the chicken muscle type enzyme did not cross-react with the chicken brain type enzyme and the rabbit muscle type enzyme. However, the hybrid enzyme reacted with both antibodies. The two brain type enzymes from the chicken and rabbit, or the two muscle enzymes, were more similar in their properties than were the brain and muscle forms of one species. The physical and chemical properties of the enzymes were determined.

(11) Glutamic oxaloacetic transaminase and

(12) Glutamic pyruvic transaminase

Chicken blood

McDaniel and Chute (1961) measured the levels of enzymes in two breeds of chicken. The enzymes measured included glutamic oxaloacetic transaminase, glutamic pyruvic transaminase, acid phosphatase, lactic dehydrogenase, malic dehydrogenase, and alkaline phosphatase.

Also see Cornelius et al. (1959)—aldolase, Class 4, p. 34;
McFarland et al. (1965)—lactate dehydrogenase,
Class 1, p. 5-6.

(13) Tyrosine aminotransferase

a. Chicken liver

Litwack and Nemeth (1965) found that in the homogenate of chicken liver the tyrosine aminotransferase activity was relatively constant during the embryonic period. After hatching, a somewhat variable 2- to 3-fold increase was observed which persisted for approximately 10 days. The activity in the homogenates of chicken liver obtained at steps during embryonic life and after hatching was relatively specific for α -ketoglutarate.

b. Chicken embryo

Knox and Eppenberger (1966) showed that in the liver of chick embryos tyrosine transaminase was present from the fifth day, tryptophan pyrrolase from the 11th day, and formylase appeared at the time of hatching. The tyrosine transaminase level was elevated 5-fold by treatment with hydrocortisone but not with tryptophan, and the tryptophan pyrrolase was similarly elevated by treatment with tryptophan but not with hydrocortisone. The developmental elevation of formylase was not affected by either treatment. The behavior of the enzymes was, therefore, markedly different in the chick embryo than in the fetal rat.

(14) Phosphoglycerate mutase

Chick muscle

Phosphoglycerate mutase was prepared from commercially available frozen chicken breast in high yield. The procedure for the preparation and the properties of the enzyme were described by Torralba and Grisolia (1966).

(15) Amidino-transferase

Chick embryo

Walker and Wang (1964) determined the relationships between liver-creatine concentration and L-arginine:glycine amidino-transferase activity in the closed system of the developing chick embryo. Creatine, or phosphocreatine, appeared to be the specific metabolite-repressor of the enzyme.

(16) Hexokinase

Chick embryo

Guidotti et al. (1964) found that in 10-day chick embryo hearts, free glucose accumulated at an extracellular concentration exceeding 24 mM. Below this concentration the inward transport of glucose conformed to a Michaelis-Menten kinetics with hexokinase $K_m=2.3 \times 10^{-2}M$ and a transport maximum of about 7 mg/g wet wt/hr.

(17) Formylglycinamide ribotide amidotransferase

(18) 5-Phosphoriboxylpyrophosphate amidotransferase

(19) Glycinamide ribotide transformylase and

(20) 5-Amino-4-imidazolecarboxamide ribotide transformylase

Chicken and pigeon liver

Flaks and Lukens (1963) in their review on the enzymes of purine nucleotide synthesis de novo, stated that avian livers have the highest known concentrations of purine synthetic enzymes of any animal tissue studied, since the pathway was utilized by birds as a means of nitrogen elimination.

(21) Transaldolase and

(22) Transketolase

See Goodridge and Ball (1966)—acetyl CoA carboxylase, Class 6, p. 37-38.

(23) NAD pyrophosphorylase

See Lee (1963)—succinate dehydrogenase, Class 1, p. 12.

(24) Choline acetylase

See Aprison et al. (1964)—hydroxytryptophan decarboxylase, Class 4, p. 34.

(25) Phosphoglucomutase

See McFarland et al. (1965)—lactate dehydrogenase, Class 1, p. 5-6.

(26) Myokinase

See Kitiyakara and Harman (1953)—ATPase, Class 3, p. 30.

3. Hydrolases

Enzymes of this group hydrolyze a variety of compounds. The following enzymes were found in the studies of birds.

(1) Aliesterases and

(2) Arylesterases

Chicken and duck blood

Electrophoresis studies on blood plasma esterases on a cellulose column showed that chicken plasma were characterized by a propionylcholinesterase. This was the only esterase present and it differed from other cholinesterases in many respects. Duck plasma contained a propionyl- β -esterase in addition to a propionylcholinesterase (Augustinsson, 1959a). Further study with 27 various vertebrates showed that arylesterase was the predominant esterase in mammalian plasma, and was absent in the plasma of chicken and duck, as well as being absent in reptiles, amphibians, and fish (Augustinsson, 1959b).

Kaminski (1964) found that duck serum contained three esterases. One of the enzymes was characterized as the cholinesterase and two others as aliesterases.

(3) Lipase

a. Chick pancreas and small intestine

Lipase and esterase activities of the pancreas and small intestine of the chick were investigated. In chicks from 1 to 30 days of age the lipase activity of the pancreas remained fairly constant, but the esterase activity of the small intestine increased markedly from 1 to 10 days of age and then remained constant. Of the three sections of the small intestine examined, lipase activity was greatest in the upper small intestine, whereas esterase activity was greatest in the duodenum. Although lipase activity was almost entirely confined to the pancreas, and esterase activity to the small intestine, evidence was given that both enzymes were present in both tissues (Laws and Moore, 1963).

b. Chick embryo

During the 8 to 19 days of incubation the lipase activity in the liver was found to increase gradually from the eighth to the 14th day, and then to shoot up suddenly, reaching the peak on the 16th day. This rise in activity was correlated with the extent of fat metabolism in the embryo during the period (George and Iype, 1962).

c. Pigeon muscle

An improved histochemical demonstration of lipase activity with pigeon breast muscle was described. The red narrow fibers contained a large concentration of lipase, while the white, broad ones did not. Tissue samples coated with gelatine improved with histochemical test for the presence of lipase (George and Iype, 1960). In the particulate fractions of the pigeon breast muscle, the soluble fraction showed highest lipase activity; mitochondrial and microsomal fractions showed only one half the activity. The specific activity of lipase, however, was found to be maximum in the microsomes (George and Talesara, 1962a). The mitochondrial lipase and SDH activities were strikingly low in the premigratory phase (George and Vallyathan, 1964). Histochemically, lipase activity was demonstrated by Bokdawala and George (1964) in pigeon breast muscle using "Tween 85" as substrate and alizarin red S as stain for the calcium soap formed.

Pope and Tidwell (1964) purified from homogenates of chicken intestinal mucosa an enzyme catalyzing the hydrolysis of mono-glycerides. It was liberated from lyophilized microsomes by treatment with sodium deoxycholate and subsequently with calcium chloride. Unlike pancreatic lipase, the activity did not seem to be promoted by taurocholate.

(4) Cholinesterases

Chick blood

Mendel et al. (1943) in a test using acetyl- β -methylcholine, which was hydrolyzed by true but not pseudo-cholinesterase and benzoylcholine as substrates, found that the plasmas of chicks, ducks, and pigeon contained true and pseudo-cholinesterases (with pigeon not conclusive in pseudo-cholinesterase). There was neither true nor pseudo-cholinesterase in their cells.

Also see Augustinsson (1959b)—aliesterases and arylesterases, p. 20;

Plimmer and Rosedale (1922)—amylase, p. 27;

Leasure and Link (1940)—amylase, p. 30;

George and Talesara (1961c)—cytochrome oxidase, Class 1, p. 14.

(5) Lactase

Chicken crop

Hamilton and Mitchell (1924) found lactase present in the crop but absent in the proventriculus, the pancreas, and the intestines of normal chickens.

Also see Plimmer and Rosedale (1922)—amylase, p. 27.

(6) Alkaline phosphatase and

(7) Acid phosphatase

a. Chicken blood

Laying hens had higher and more variable serum phosphatase than cocks. No great difference in serum phosphatase could be found between laying hens and hens in a period of suspended egg production. Pullets from another source which had never laid gave values comparable with the value for cocks. Serum phosphatase was much higher in chicks suffering from rickets (Common, 1936). The acid phosphatase activity was about equal in the erythrocyte cells of birds and turtles, while alkaline phosphatase activity in these cells was variable (Rapoport et al., 1942). Stutts et al. (1957), who studied plasma alkaline phosphatase activity in mature inbred chickens, believed that differences in alkaline phosphatase activity in blood indicated that the phosphatase level was in part genetically controlled. In each line the enzyme activity of females was higher and more variable than that of the males.

Tanabe and Wilcox (1960) found that serum alkaline phosphatase in chickens was higher in most cases between 2 and 26 weeks of age in a line bred for high alkaline phosphatase than in a random bred control line. The level in the male was higher than the female during the growing period, but lower at later age. There were no differences at hatching due to the line or sex. Bell (1960) found in his study with Brown Leghorns that both adult nonlaying hens and cocks showed enzymatic activity of the same order. The plasma of the mature birds (5 to 6 weeks old) of both sexes had alkaline phosphatase levels up to 10X those found in nonlaying adults. In the hen, the average level of plasma enzymatic activity was increased by about 50 percent when hens began to lay. The massive temporary increase in plasma phosphatase shown by the laying hens was believed to reflect a stimulation of the osteoblastic recalcification process called into action by the drain on skeletal calcium required for egg shells. Bell (1961) studied the plasma acid phosphatase activity and bone dystrophies in the domestic fowl

and found that fowls with severe osteoporosis, where many osteoclasts were present, usually showed an elevated plasma acid phosphatase activity as well as greatly raised alkaline phosphatase activity.

Dounce and Seibel (1943) found the enzyme acid phosphatase in nuclei isolated from washed chicken erythrocytes. The activity of fresh preparations determined by the use of disodium phenylphosphate as substrate corresponded to the liberation of about 0.0025 to 0.0030 mg of phenol from the substrate per milligram of tissue per hour at 25°C. Approximately the same concentration of enzyme was found in the washed whole erythrocytes. Hurwitz and Griminger (1961) conducted experiments to evaluate the relationships between plasma alkaline phosphatase and plasma inorganic phosphorus, bone constituents, and parathyroid size. They found that calcium-deficient hens, irrespective of supplementation with phosphorus, have enlarged parathyroids, elevated plasma alkaline phosphatase, and loss of bone material. The experimental results indicated that decalcification rather than calcification of bone was associated with increased alkaline phosphatase levels.

b. Red-winged blackbird brain

Rogers (1963a) used red-winged blackbird and chick (*Gallus*) in his comparative biochemical alkaline phosphatase studies in relation to brain development. The enzyme levels of red-wing were determined in three brain parts during the 15 days after hatching; those of chick were determined at the 19th embryonic day, 6 days and 9 weeks after hatching. Redwing enzyme increase in the posthatching period was similar to that of chick brain in the late embryonic period. Enzyme levels in both birds decline in adult after a peak was reached. The author believed that the results supported the hypothesis that alkaline phosphatase played a role in the differentiation of the central nervous system. Rogers (1963b) also histochemically localized the enzyme in the brains of chick, red-wing and other mammals. He found that the results contained data both for and against the association of alkaline phosphatase and myelination in the late development of the nervous system.

Wilson and Wilcox (1963) determined the origin of the increased serum alkaline phosphatase in chicks by means of enzyme inhibition studies. Both high phosphatase line and random bred line of chicks were investigated. Sodium borate was found to rather selectively inhibit the serum phosphatase in the high line. Further studies with this inhibitor on tissues from both lines of chicks showed that intestinal phosphatase activity was inhibited to a much greater degree than that

in bone, liver, and kidney. These studies indicated to the authors that the major portion, if not all, of the increased serum phosphatase of the high line originated in the intestine.

The influence of dietary minerals on the pH optima and reaction velocities of phosphatases of the chicken was studied using magnesium, calcium, and molybdenum ions (Motzok, 1963).

c. Duck pancreas

Enzyme histochemical study of the pancreatic islets in duck showed that the islet B cells exhibited a strong reaction for alkaline phosphatases, but a weak one for acid phosphatase. The activities of G-6-Pase, ATPase, diphosphopyridine nucleotide diaphorase, triphosphopyridine nucleotide diaphorase, and β -hydroxybutyrate dehydrogenase also were positive. Amino-peptidase and esterase activities were not found in the B cells, however (Hellerström, 1963).

d. Chick embryo

Moog and Richardson (1955) showed that the duodenum of the chick embryo was characterized by a high level of alkaline phosphatase activity. Precocious phosphatase accumulation induced by corticoid administration was accomplished by equally precocious differentiation of the epithelial cells of duodenum. The authors suggested that the functional differentiation of the small intestine was normally controlled by secretions from the cortical material of the embryo's own adrenal glands.

Salzgeber and Weber (1966) determined acid phosphatase and cathepsin activity and total nitrogen in the homogenates of chick embryo mesonephros during growth and regression. The loss of total nitrogen in this period was as much as 62 percent. Specific acid phosphatase activity increased appreciably during regression.

e. Chick oviduct

Administration of exogenous estrogen diethyl-stilboestrol dipropionate caused an increase in the alkaline phosphatase activity of chick oviduct. Graded doses of estrogens caused a relative increase in the alkaline phosphatase activity of the oviduct which was significantly proportionate to the dose of estrogen (Pande et al., 1966).

f. Isozyme study with alkaline phosphatases

Characterization of alkaline phosphatases of the chick to ascertain the origin of the serum enzymes and the enzymatic

relationship to calcium metabolism was made by Kuan et al. (1966). Fractionation by ammonium sulfate precipitation and ion exchange column chromatography were conducted. From observations of the above experiments and determinations of enzyme concentrations of the serum, bone, intestine, and liver at various ages after hatching, the authors concluded that the serum alkaline phosphatase isozymes originated from bone. The chromatographic separation of proteins with enzyme activity from bone behaved more like those of the serum than those of the intestine and the liver.

Also see Maddaiah et al. (1964)—phytase, p. 25;
Hijmans and McCarty (1966)—invertase, p. 28;
Hinsch (1966)—ATPase, p. 31;
McDaniel and Chute (1961)—glutamic oxaloacetic
transaminase, Class 2, p. 18.

(8) 5'-Nucleotidase

Chicken muscle

The suitable conditions for the assay of 5'-nucleotidase activity in chick skeletal muscle were described by Roffler et al. (1966). They found that both calcified and normal chick muscles were extremely low in enzyme activity.

Also see Hinsch (1966)—ATPase, p. 31.

(9) Phytase

Chicken intestine

Maddaiah et al. (1964), using calcium phytate and sodium phytate as dietary phosphorus sources, measured the intestinal phytase activity in chicks and mature hens. The measurement failed to show a significant difference in the activity of this enzyme due to the dietary treatments. It only indicated that the phytase activity might have been due to a nonspecific phosphatase in the intestinal homogenates.

(10) Glucose-6-phosphatase

Chick embryo

Hepatic glucose-6-phosphatase activity was found in developing chick embryo almost simultaneously with the appearance of the first hepatic cells. G-6-Pase and β -glucuronidase activity of the embryo increased in direct proportion to liver weight. Properties of embryonic liver G-6-Pase were similar to those found in adult liver of other species. Studies with liver

slices indicated that the embryo liver was capable of glycolysis and glucose formation (Kilsheimer et al., 1960).

The effect of cortisone and hydrocortisone on glucose-6-phosphatase activity in the chick embryo liver was studied by Ogorodnikova (1965). Both hormones increased the activity of the enzyme.

Also see Hellerström (1963)—alkaline and acid phosphatases, p. 24;
Hinsch (1966)—ATPase, p. 31.

(11) Phosphoproteinphosphatase

a. Chick embryo

Phosphoproteinphosphatase from chicken embryos completely split off alkaline-labile phosphorous from casein and the Alkaline-labile phosphorous in brain phosphoprotein (Fedorova and Komkova, 1964).

b. Chicken and pigeon muscle

Bargoni et al. (1963) found phosphoproteinphosphatase in the soluble part of chicken and pigeon muscle cells.

(12) Phosphodiesterase

Chicken bone marrow

Bristow and Yamada (1965) found phosphodiesterase as well as an acid phosphatase in the marrow of White Leghorn chickens. Some properties and the intracellular distribution of these two enzymes were described.

(13) Serine ethanolamine phosphate phosphodiesterase

Chicken kidney

Hagerman et al. (1965) purified serine ethanolamine phosphate phosphodiesterase from chicken kidney. They believed that in conjunction with kidney phosphomonoesterase, the new diesterase accounted for the degradative metabolism of the diester.

(14) Deoxyribonuclease I and

(15) Deoxyribonuclease II

Chick embryo

The in vitro activity of deoxyribonuclease I and deoxyribonuclease II was determined in the embryo and in the allantoic

fluid of the chick during the 6th to 16th day of development within the egg. The respective increases in activities and the successive changes in the ratios of activities of deoxyribonuclease I/deoxyribonuclease II were reported (Tempel and Zipf, 1966).

(16) Amylase

a. Chicken alimentary canal

A study on the distribution of enzymes in the alimentary canal of the chicken showed the presence of amylase, invertase, lactase, lipase, and proteolytic enzymes (Plimmer and Rosedale, 1922).

b. Chicken saliva

Amylase always was present in the saliva of mature hens, lipase was present but relatively inactive, salivary proteinase was negligible or absent, and rennin was not present (Leasure and Link, 1940).

c. Chicken bile and liver

An amylase which was secreted by the liver was found in chicken bile. Its optimum hydrogen ion concentration was similar to that of pancreatic amylase (Farner, 1943).

d. Chicken blood

Serum amylase activity in chickens was depressed by cholera infections (Squibb et al., 1955).

e. Chick embryo

The growth pattern of the chick embryo was related to α -amylase activity in the developing pancreas. The steepest rise in amylase activity coincided with the period of rapid growth and increase in cell size which overlapped the time of hatching (Kulka and Duksin, 1964). When stimulated by cholinergic drugs, the pancreas taken from chick embryos would secrete amylase in vitro. The pancreas evidently acquired the ability to secrete digestive enzymes more than 10 days before the beginning of the prominent biochemical and morphological changes associated with the maturation of the gland (Kulka and Yalovsky, 1966).

(17) Invertase

a. Chicken muscle

Invertase was present in the glycerine extracts of the chicken gizzard muscle, the mucous membrane of the gizzard, and in the thigh and breast muscle (Bernardi and Schwarz, 1932).

b. Chick embryo

Hydrocortisone induced the activity of alkaline phosphatase and invertase but not lactic dehydrogenase in chick embryo duodenum culture. The authors suggested that hormones might act as specific inducers of genetic transcription of the synthesis of a number of enzymes, and that some hormones might also have an action on some step in protein synthesis beyond the level of genetic transcription (Hijmans and McCarty, 1966).

Also see Plimmer and Rosedale (1922)—amylase, p. 27.

(18) Carboxypeptidase

Chicken blood and lymph

Erdoš et al. (1964) described a carboxypeptidase which existed in the blood sera of birds, mammals, amphibia, and other animals; in lymph; in human urine and thrombocytes; but not in erythrocytes. No significant enzyme activity was seen in human serum.

(19) Pepsin

Chicken and pigeon gastric mucosa

Friedman (1939) reported that with respect to acid and pepsin, the chief difference between mammals and birds was that in birds (chicken and pigeon) both substances were produced by the same type of cells, while in mammals each was produced by one particular kind of cell—two morphologically different elements of the mucosa of the stomach. The concentration of pepsin was higher in the gastric juice of the chicken than in that of the pigeon. Levchuk and Orekhovich (1963) purified pepsinogen from chick gastric mucosa extract by means of ion exchange column chromatography. Three pepsins were obtained. Some of their hydrolytic properties were described.

(20) Trypsin and

(21) Chymotrypsin

a. Sea gull

Farner (1960), in his review on the digestion and digestive system of birds, stated that trypsin and intestinal enterokinase had been reported from the sea gull. He also stated that protein digestion in birds, like so many other aspects of avian digestion, needed extensive investigation.

b. Turkey and chicken

Purified turkey trypsin behaved in much the same manner as bovine trypsin, both toward substrates and inhibitors. Chicken chymotrypsin, however, exhibited some unusual behavior toward natural and synthetic substrates as well as some naturally occurring protease inhibitors. The differences in the reactivity between chymotrypsins from avian and mammalian origins toward the ester and protein substrates tested probably were due to primary or secondary structural variations that were expressions of natural mutations (Ryan and Clary, 1964). Chicken chymotrypsin and turkey trypsin were further purified (Ryan, 1965). Turkey trypsin reacted with substrates and inhibitors in the same manner as mammalian trypsins. The enzyme was stabilized by calcium at low and neutral pH.

The amino acid analysis also indicated a similarity to mammalian trypsins. Chicken chymotrypsin showed esterase activity twice that of bovine α -chymotrypsin but only two-thirds of the protease activity. Calcium did not increase the esterase activity but did stabilize the enzyme near pH 7. At a low pH, the enzyme was more stable in the absence of calcium. Results indicated that natural variations between chicken and mammalian chymotrypsins occurred in both physical and enzymatic properties, whereas variations between turkey and mammalian trypsins were confined almost entirely to physical properties (Ryan et al., 1965).

c. Turkey ovomucoid

Simlot and Feeney (1964) showed that turkey ovomucoid inhibited both trypsin and chymotrypsin and that the enzymes occurred at independent sites.

(22) Elastase

Chick sera

Walford and Schneider (1959) presented the percent of inhibition of elastase in chicken sera.

(23) Arginase

Bird liver and kidney

Hunter and Dauphinee (1924) showed that arginase was absent in the livers of birds but present in their kidneys. Dounce (1950), however, stated that arginase activity was zero in chicken liver cell nuclei. Cohen and Brown (1960), in their comment on ammonia metabolism and urea biosynthesis, stated that the location of arginase in the avian kidney instead of the liver might serve to minimize the breakdown of arginine. Arginine is an essential amino acid for birds. The presence of arginase in kidney serves to provide ornithione for the detoxication of benzoic acid.

Brown (1966), using more precise techniques, further demonstrated that arginine occurred in the liver of numerous birds. The stoichiometry of the reaction was demonstrated, and the urea formed was derived from the amidine group of arginine. A relatively high level of arginase activity was found in the liver of some birds—kingfishers, herons, and gulls. The lowest activity occurred in the liver of chickens and pigeons.

(24) Inorganic pyrophosphatase

Pigeon pancreas

Pynes and Younathan (1964) reported that the supernatant fraction of the pigeon pancreas contained one of the highest inorganic pyrophosphatase activities reported for tissues of higher animals. The existence of this enzyme in the pancreas had not been reported previously.

(25) ATPase

a. Pigeon muscle

Kitiyakara and Harman (1953) centrifugally fractionated pigeon breast muscle and analyzed the distribution of enzyme activity among the different particles. Magnesium-activated ATPase (adenosinetriphosphatase) and myokinase were found to be located predominantly in the cy tochondria. The myofibrillar nuclear components were the sites of calcium-activated ATPase and adenylic acid deaminase. Chappell and Perry (1953) showed that pigeon-breast mitochondria contained an ATPase which was activated to a greater extent by Mg^{++} than by Ca^{++} .

b. Chicken muscle

Tonzetich and Kare (1960) differentiated adenosinetriphosphatase preparations obtained from two muscle sources of hen

muscle on the basis of their solubility. An active ATPase was extracted with water from the red muscle, but not from the white. Active preparations from both muscle sources were soluble in dilute KCl. The KCl extracts of the water-insoluble white-muscle sediment yielded ATPase activity comparable to the direct KCl extracts. Dialysis of the enzyme preparations failed to remove any factor necessary for ATPase activity.

c. Chick embryo

Klein (1963) studied the ATPase of isolated mitochondria and microsomes from embryonic chick ventricles at different stages of development. He demonstrated a typical myocardial cation transfer ATPase in the microsomal fraction.

d. Pigeon brain

The microsomal ATPase prepared from pigeon brain was activated by Mg but little by Na and K. Twenty micromolar Cu achieved maximum inhibition, reducing enzyme activity by approximately 25 percent. It was found that there were at least three components in the pigeon's brain microsomal ATPase (Peters et al., 1966). Peters and Walsh (1966), in their study of the toxic action of copper using pigeon and rat brains, found that the highest affinity for copper was in an ATPase-rich microsomal fraction.

e. Chick esophagus and trachea

Tissues of chick embryos (17 to 45 days) and chicks (1 day to 3 weeks of age) were frozen and sectioned. Adenosinetriphosphatase, 5'-nucleotidase, acid phosphatase, nonspecific esterase, nonspecific glycerophosphatase, nucleotide-diphosphatase, and glucose-6-phosphatase were localized in these tissues (Hinsch, 1966).

f. Herring gull salt gland

Bonting et al. (1964) found Na-K-activated ATPase to a high degree in the salt gland of the herring gull. The properties of the enzymes were described.

Also see Lee (1963)—succinate dehydrogenase, Class 1, p. 12;
Hellerström (1963)—alkaline and acid phosphatases,
p. 24.

(26) Apyrase

Chicken blood

Frank et al. (1950) studied apyrases derived from chicken blood. The enzyme activities were high in chicken red blood

cells and were associated with nuclei. The pH-activity curve differed markedly among species. Magnesium ions stimulated the activity of the chicken blood plasma uniformly throughout the pH curve.

(27) Deoxycytidylate deaminase

Chick embryo

Maley and Maley (1963, 1964a) reported the purification and properties of deoxycytidylate deaminase recovered from 6-day-old chick embryo extract. The activity of the enzyme depended upon the presence of deoxycytidine triphosphate and magnesium ions. The authors suggested that thymidylate biosynthesis from deoxycytidylate was regulated by end products associated with its metabolic pathway, dCTP and dTTP. Later (1964b) they showed that the activation effect by dCTP was associated with an alteration in the structure of the enzyme.

(28) Fluoroacetanilide amidohydrolase

Chick liver

Nakamura et al. (1966b) extracted fluoroacetanilide amidohydrolase from the mouse and chick livers and compared their basal properties. Enzymes from both sources were inhibited by reagents that react with sulfhydryl group and chelate with metallic ions, and their properties were mutually coincidental. Nakamura et al. (1966a) studied the chick enzyme further. It hydrolyzed monohaloacetanilides, iodoacetanilide and chloroacetanilide, beside fluoroacetanilides, but it had no activity with acetanilides. It was a metal enzyme containing a tightly bound metal ion. The activity of the enzyme was increased by Mn^{++} , Mg^{++} , Co^{++} , Ba^{++} , and Ca^{++} and was decreased by Zn^{++} and Ni^{++} .

(29) Adenosine deaminase

Chick

Chilson (1963) prepared chicken and calf adenosine deaminase. He found subtle differences in the rate at which deoxyadenosine was deaminated and more striking differences with the substrates 2-fluoroadenosine and 2,6-diaminopurine nucleoside. Also, the temperature effect on the chicken's enzyme was different from that on the calf's.

(30) β -Glucuronidase

See Kilsheimer et al. (1960)—glucose-6-phosphatase, p. 25-26.

- (31) Adenylic acid deaminase
See Kitiyakara and Harman (1953)—ATPase, p. 30.
- (32) Phosphomonoesterase
See Hagerman et al. (1965)—serine ethanolamine phosphate phosphodiesterase, p. 26.
- (33) Acetylcholinesterase
See Aprison et al. (1964)—hydroxytryptophan decarboxylase, Class 4, p. 34.
- (34) Uronolactonase
See Reithel (1967)—glucuronolactone reductase, Class 1, p. 2.
- (35) Formylase
See Knox and Eppenberger (1966)—tyrosine transaminase, Class 2, p. 18.
- (36) ATP pyrophosphatase
See Lee (1963)—succinate dehydrogenase, Class 1, p. 12.
- (37) Nucleotide-diphosphatase
See Hinsch (1966)—ATPase, Class 3, p. 31.
- (38) Fructose-diphosphatase
See Krebs (1964)—pyruvate carboxylase, Class 6, p. 37.
- (39) Lactonase
See Goodridge and Ball (1966)—acetyl CoA carboxylase, Class 6, p. 37-38.

4. Lyases

Enzymes of this group catalyze the removal of groups from substrates without hydrolysis. They leave double bonds or conversely, add groups to double bonds.

(1) 5-Hydroxytryptophan decarboxylase

Pigeon brain

Activities of 5-hydroxytryptophan decarboxylase, choline acetylase, acetylcholinesterase, and monoamine oxidase were determined in the telencephalon, diencephalon, plus optic lobes, cerebellum, and ponsmedulla oblongata of young adult pigeons. A comparative study of the enzymes was conducted (Aprison et al., 1964).

(2) Aldolase

a. Chicken plasma

Cornelius et al. (1959), noticed a pronounced elevation of plasma aldolase activity occurring in all birds exhibiting dystrophy. The glutamic-oxaloacetic transaminase activity also increased.

b. Pigeon muscle

George and Talesara (1962b) demonstrated histochemically the presence of a high concentration of aldolase in the broad, white glycogen-loaded fibers.

Also see McFarland et al. (1965)—lactate dehydrogenase, Class 1, p. 5-6;
Rinaudo (1962)—phosphohexoisomerase, Class 5, p. 36.

(3) Citrate cleavage enzyme

a. Chicken blood

The oxygen consumption of the avian erythrocyte involved the mechanism of the tricarboxylic acid cycle; all tricarboxylic acid cycle enzymes were present except a specific oxalacetic decarboxylase (Rubinstein and Denstedt, 1953).

b. Chicken liver

Srere and Bhaduri (1964) reported the purification and properties of the citrate cleavage enzyme from chicken liver.

Also see Goodridge and Ball (1966)—acetyl CoA carboxylase, Class 6, p. 37-38.

(4) Carbonic anhydrase

Chicken oviduct

Common (1941) suggested that the carbonic anhydrase activity of the uterine epithelium of hen was higher than that of the

remaining oviductal tissues, and that this activity might play a part in shell secretion. Gutowska and Mitchell (1945) reported that carbonic anhydrase seemed to be one of the active factors in the enzymatic system of calcification of the egg-shell. It liberated the anion, but not the cation, needed in this process. The same hens could be made to lay either strong-shelled, or soft-shelled eggs, or rough-shelled eggs by inhibiting the activity of carbonic anhydrase by subcutaneous sulfanilamide injection. The authors proposed that this enzyme acted in the shell gland as a catalyst for decomposition of carbonic acid, which might form bicarbonate ions from the blood; these carbonate ions then were utilized in calcium carbonate deposition. Robinson and King (1963) demonstrated histologically that carbonic anhydrase was concentrated at the mammillae of shell membrane.

Also see Bonting et al. (1964)—ATPase, Class 3, p. 31.

(5) D-Serine dehydratase

Chicken kidney

Grillo et al. (1965) partially purified D-serine dehydratase from chicken kidney. Some general properties and activators were reported.

(6) Cysteine synthetase

Chicken embryo (vitellin sack and liver)

Sentenac and Fromageot (1964) reported the presence of serine-hydrolyase in the vitellin sack and the liver of chicken embryo. This enzyme catalyzed the synthesis of cysteine from serine and mineral sulfide.

(7) Phosphopyruvate dehydratase

Chicken embryo

Rinaudo (1962) studied the glycogenesis in the liver of chicken embryo. Phosphopyruvate dehydratase, glyceraldehyde-3-phosphate dehydrogenase, aldolase, and phosphohexoisomerase were assayed. These enzymes behave differently from one another during the 6th to 20th day observed during the incubation, but they all had one or two maxima of activities on or between the 12th and the 18th days. After the 20th day all the activities dropped. The author believed that his experimental data suggested the reversal of anaerobic glycolysis as the pathway for the glycogenesis from pyruvate in the liver of chicken embryo.

(8) 5-Aminoimidazole ribotide carboxylase

(9) 5-Amino-4-imidazole-N-succinocarboxamide ribotide cleavage enzyme and

(10) Inosinicase

Chicken and pigeon liver

The above are the lyases among the enzymes of purine nucleotide synthesis as given in the review by Flaks and Lukens (1963).

(11) Fumarase and

(12) Aconitase

See Rubinstein and Denstedt (1953)—citrate cleavage enzyme, Class 4, p. 34.

(13) Enolase

See Rinaudo (1962)—phosphohexoisomerase, Class 5, p. 36.

5. Isomerases

The enzymes in this group catalyze various types of isomerization. They can be subdivided into racemases, epimerases, cis-trans isomerases, intramolecular ketol isomerases, and intramolecular transferases.

(1) Phosphohexoisomerase

Chick embryo

Rinaudo (1962) reported the activity of phosphohexoisomerase in the chicken embryo liver.

(2) Methylmalonyl-CoA mutase

Chick liver

A vitamin B₁₂ deficient liver evidenced lower methylmalonyl-CoA mutase within 3 weeks in chicks. Isotopic tracings showed that the hydrogen atom transfer that occurred during the mutase reaction originated in the methyl group of methylmalonyl CoA (Erfle et al., 1964).

(3) Phosphopentoeptimerase and

(4) Phosphoriboisomerase

See Goodridge and Ball (1966)—acetyl CoA carboxylase, Class 6, p. 37-38.

6. Ligases

This group of enzymes catalyze the linking together of two molecules with the breakdown of a pyrophosphate bond in ATP or a similar triphosphate.

(1) Pyruvate carboxylase

a. Pigeon liver and kidney

Krebs (1964) in his 1963 Croonian lecture on "Gluconeogenesis" mentioned that experiments on pigeon liver homogenates and kidney cortex slices indicated that feedback control occurred in the stage of pyruvate carboxylase and fructose-diphosphatase.

b. Chicken liver

Keech and Utter (1963) and Utter and Keech (1963) showed that intracellularly pyruvate carboxylases appeared to be associated with the particulate matter of avian liver cells. The characteristics of the enzyme were described. The enzymatic reaction did not appear to be related to the CO₂-fixing reaction. Later work showed that this enzyme catalyzed an ATP- and acetyl CoA-dependent fixation of CO₂ with pyruvate to form oxaloacetate. The enzyme contained biotin (Scrutton and Utter, 1964). The method which permitted the preparation of relatively large quantities of pyruvate carboxylase from chicken liver mitochondria was described. Some physical and chemical properties of the highly purified enzyme were also described (Scrutton and Utter, 1965).

(2) Acetyl CoA carboxylase

a. Chicken liver

Numa et al. (1966) prepared acetyl CoA carboxylase from chicken liver. A correlation between activation of the carboxylase and an increase in its sedimentation coefficient was shown.

b. Pigeon adipose tissue

Goodridge and Ball (1966) found low activities of acetyl CoA carboxylase, citrate cleavage enzyme, malic enzyme, and hexose monophosphate shunt dehydrogenases in the homogenates of pigeon adipose tissue, but very high activities of those enzymes, except for shunt dehydrogenases, in the homogenates of pigeon liver, about 4 to 20 times higher than those in rat liver. They also found that the marked effect of starvation and refeeding on the enzyme activities of liver and adipose tissues of rats was not present in those of pigeon. Since these enzymes were involved in lipogenesis, the authors believed that pigeons adipose tissue might be much less active in de novo lipogenesis

than rat adipose tissue and might serve largely as a depository for fat synthesized elsewhere. They suggested that liver might be the chief site of fatty acid synthesis in pigeons. Waite and Wakil (1966) showed by using the criterion of the degree of binding of the biotin derivatives to avidin that these compounds had an intact ureido ring, thus eliminating the diamine derivative as an intermediate in the carboxylation.

(3) Glutamine synthetase

Pigeon liver

Sasaoka et al. (1964) discussed the possible presence of glutamine synthetase in pigeon liver because of its ability to synthesize theanine from glutamic acid and ethylamine in the presence of ATP.

(4) Glycinamide ribotide kinosynthase

(5) Formylglycinamide ribotide kinocyclodehydrase and

(6) 5-Amino-4-imidazole-N-succinocarboxamide ribotide kinosynthase

Chicken and pigeon liver

The above were the ligases among the enzymes of purine nucleotide synthesis as given in the review by Flaks and Lukens (1963).

(7) Succinyl CoA synthetase

See Rubinstein and Denstedt (1953)—citrate cleavage enzyme, Class 4, p. 34.

II. Miscellaneous Enzymatic Reactions

This section reports those works on enzymatic activities in which the authors did not specify the enzymes or enzyme systems. The subject matter is arranged chronologically according to the date of publication.

Cyclophorase

The skeletal bird muscles which were used only sporadically generally had relatively low cyclophorase activity and a low mitochondrial count, whereas muscles which had to function either continuously or for prolonged periods have a high cyclophorase activity and an abundance of mitochondrial units (Paul and Sperling, 1952).

Dipeptidase

The nucleated erythrocytes of birds had a higher dipeptidase content than that of the anucleated erythrocytes of mammals (Salvidio and Urbani, 1954).

Carbohydrate metabolism

Chicken liver differed from rat liver in three things: 1. sucrose enhanced the oxygen uptake of chicken liver slices incubated in a saline buffered with phosphate but not those of rat liver, 2. sorbitol did not support chicken liver respiration as it did rat liver, and 3. the fructose metabolism end products were different. The chicken end product was 1- α -glycerophosphate while the rat end products were dihydroxyacetone phosphate and glyceraldehyde (Heald, 1962). Slices of chicken liver metabolized fructose with an increased oxygen uptake, in contrast with mammalian liver where fructose metabolism did not increase the oxygen uptake. The RQ (respiratory quotient) was 1.1. Slices of pigeon liver also showed an increased oxygen uptake, but RQ not greater than 1.0 (Heald, 1963).

Esterases

Starch-gel electrophoresis was used in the study of the tissue- and species-specificity of esterases. Chicken esterases exhibited entirely different zymogram patterns from those of other species and were highly reproducible (Paul and Fottrell, 1961). In agar electrophoresis the esterase activity of duck serum was found to localize mainly in the region of α -globulin (Kaminski and Gajos, 1963). The esterases activity was further characterized by Kaminski (1964). The isozyme patterns of chicken pancreas were compared with those prepared from serum and liver. The esterase patterns were found to be organ specific, but the electrophoretic patterns for the splenic pancreatic lobe and the ventral lobe showed no differences. A marked esterase reaction along the capillaries of the A cell islets was noted (Hellman and Beckman, 1963).

Ribonucleic acid polymerase

In the study of the effect of estradiol injections upon chicken liver nuclei ribonucleic acid polymerase, Weill et al. (1963) found that after injection with estradiol, no change in composition of the synthesized RNA could be detected through comparison of carbon-14 adenosine triphosphate and carbon-14 CTP incorporations. In addition, the ratio of these incorporations was different from the CMP to AMP ratio in chicken liver deoxyribonucleic acid.

Metalloporphyrin-forming enzymes

Metalloporphyrin-forming enzymes were found in the extracts of avian erythrocytes. While liver mitochondrial extract readily catalyzes the incorporation of Fe^{2+} and Co^{2+} into protoporphyrin, the extract of avian erythrocyte only catalyzes the incorporation of Fe^{2+} (Johnson and Jones, 1964).

Fatty acid synthetase

The independent binding of the acetate and malonate moieties of acetyl and malonyl coenzyme A to a pigeon liver fatty acid synthetase through thioester bonds was demonstrated. The evidence supported a scheme of fatty acid synthesis which involves the stepwise addition of two carbon units from malonyl-enzyme to acyl-enzyme with the formation of β -ketoacyl-enzyme (Brodie et al., 1964).

Acylating enzymes

Pigeon pancreas microsomal and mitochondrial fractions catalyzed the formation of phosphatidylinositol from fatty acid thioesters of coenzyme A and lysophosphatidylinositol. An easy method was described (Keenan and Hokin, 1964).

Sacharide polymerase

A cell-free enzyme preparation was obtained from chick embryo epiphyses. It catalyzed the synthesis of a high molecular weight polysaccharide from uridine 5'-diphosphate-N-acetyl-D-galactosamine, or UDP-N-acetyl-D-glucosamine and UDP-D-glucuronic acid. When the particulate enzyme was washed twice, the UDP-GalNAc pyrophosphorylase and UDP-GlcNAc-4'-epimerase were removed, while the polymerase activity was retained (Perlman et al., 1964).

Anserine-hydrolyzing enzyme

The anserine-hydrolyzing activity in serum and acetone fraction prepared from pectoral muscles, leg muscles, livers, and kidneys of Japanese quail and variously-aged chickens was investigated and the activity was recognized in the kidney. The enzyme also hydrolyzed carnosine and orphidine (Ishikawa et al., 1964).

Benzoylornithines synthesizing enzymes

The synthesis of monobenzoylornithine and ornithuric acid in the presence of benzoic acid, ornithine, adenosine triphosphate, and coenzyme A was catalyzed by an enzyme system prepared from chicken kidney. Preliminary fractionation studies suggested the involvement of at least three enzymes in the over-all reaction (Marshall and Koepe, 1964).

Glycogen synthetase

See Fridland and Nigam (1965)—phosphorylase, Class 2, p. 16.

Glycyl-soluble-RNA synthetase

A glycyl-soluble-RNA synthetase was prepared from chick embryo. It catalyzed a glycine-dependent $^{32}\text{P}_i$ --ATP exchange but not $^{32}\text{P}_i$ --ATP exchange, and the formation of glycyl-soluble-RNA. The enzyme required either Mg^{2+} or Mn^{2+} for activity; Mg^{2+} was more effective at high concentration and Mn^{2+} at low concentration. Ca^{2+} antagonized the action of Mg^{2+} (Bublitz, 1966).

Amylase

Omission of Ca^{2+} from the incubation medium completely prevented the acetylcholine-stimulated release of amylase into the incubation medium. The omission caused some increase in the incorporation of phosphorus-32 into the lipides (Hokin, 1966).

Long-chain acyl desaturase

Analysis of the fatty acid formed in the in vitro synthesis by microsomal and soluble enzymes of pigeon liver showed that the long-chain acyl desaturase activity was eliminated by 72 hours of starvation (Butterworth et al., 1966).

Dehydrogenases and hydrolases

Electrophoretic zymograms were prepared from the aqueous extracts of breast muscle, leg muscle, cardiac muscle, liver, kidney, and spleen of adult cockerels. A partial characterization of the tissue esterases was carried out with various substrates and specific inhibitors. The 18 bands of esterases were aliesterases of two different types. Tissue-specific enzymatic patterns were obtained for esterases, alkaline phosphatase, acid phosphatase, lactate dehydrogenase, malate dehydrogenase, and isocitrate dehydrogenase. Glutamate dehydrogenase and glucose-6-phosphate dehydrogenase activity were detected only in the liver and kidney (Ecobichon, 1966).

Cathepsin

See Salzgeber and Weber (1966)—phosphatase, Class 3, p. 24.

DISCUSSION

This survey has shown that most of the work done on enzymes in birds was incidental to other objectives. Little research has been devoted exclusively to the study of enzymes or enzyme systems in birds, with the objective of obtaining a better understanding of bird metabolism. Birds used in research were mostly domestic—chickens in many cases, and sometimes pigeons, either domestic or wild. The tissues studied most were muscles and liver.

Of the 120 enzymes surveyed, oxidoreductases and hydrolases are the two classes investigated most thoroughly. All the enzymes in the pentose shunt and citric acid cycle have been reported in the literature. α -Ketoglutarate dehydrogenase, however, is not listed in APPENDIX B because it is actually an enzyme complex. Of the enzymes related to nitrogen metabolism in birds, references could be found only on those associated with nucleotide metabolism. Enzymes involved in nitrogen metabolism are of much interest in bird control because instances have been

found of the diversity in nitrogen metabolism among species. These differences, when discovered, might be exploited for the purpose of selective toxication. It is regrettable, therefore, that no useful data on these enzymes in birds could be found.

Some comparison of the degree of intensity of enzymatic activities among species have been found, but the works have been few. During recent years, comparative enzymology has been exploited as a means of taxonomy (e.g., Wilson and Kaplan, 1964). Such attempts with birds have been made especially with lactate and malate dehydrogenases. Study in this area is still quite limited, however.

Since birds are said to differ characteristically from mammals in excreting uric acid instead of urea as a waste product, a fundamental difference in the nitrogen metabolism including the urea cycle must exist between the two classes. Indeed, studies had been made to locate and quantify arginase, but enzymes in the urea cycle have not been investigated thoroughly. A study of bird metabolism and the enzymes concerned would most likely yield enlightening results.

This survey also revealed that although comparative studies on the enzyme biochemistry of birds are carried out sporadically, the number of species investigated has, indeed, been small. As a whole, the field of the comparative enzyme biochemistry of birds remains a virgin land. It is understandable, therefore, that no such study has ever been conducted on the species of birds that we are most interested in controlling. Such comparative data are very important to our development of selective toxicants for nuisance birds.

While Williams (1958) and Florkin (1960) reported on the biochemical individuality and the unity and diversity in biochemistry, and Dixon and Webb (1958), Dittmer (1961), and George and Berger (1966) tabulated and mentioned some enzymes found in birds, it has remained for this survey to collect and compile the available data on enzymes in birds covering a wider area, giving more detail about individual enzymes concerned, in order to facilitate intra- and inter-species comparison.

SUMMARY

Enzymes which appear in the literature concerning research with birds have been surveyed and reported in the six classes that were recommended in 1964 by the International Union of Biochemistry. The pertinent biochemistry is described for each enzyme. A total of 120 enzymes was surveyed.

The major comparative aspects of enzymes are as follows:

1. Avian livers have the highest known purine synthetic enzymes of any animal tissue studied.

2. Malate oxidase, succinoxidase and malate dehydrogenase are more active in bird erythrocytes than in those of higher vertebrates.
3. Birds have the highest levels of D-phosphoglycerate dehydrogenase.
4. Chicken livers differ qualitatively and quantitatively from rat livers in metabolizing fructose. Oxygen uptake did not increase in the mammalian metabolism of fructose.
5. Arginase, the enzyme which catalyzes the change of L-arginine to L-ornithine and urea, occurs in bird kidneys instead of livers as it does in other animals.
6. Contrary to mammals, ornithine transcarbamylase is either low or not detectable in birds by present methods of assay.
7. Chicken heart mitochondrial malate dehydrogenase is devoid of tryptophan as is that of pig and horse.
8. The red-whiskered bulbul (*Aves*), like the guinea pig, does not have the microsomal enzymes necessary in the synthesis of ascorbic acid.
9. Hummingbirds and swifts heart extracts have a different zymogram pattern of the "supernatant" form of malate dehydrogenase from that of chicken enzyme on gel electrophoresis; all families of Charadriiformes have an enzyme that moves more slowly than that of chicken enzyme.
10. Mammalian oxidase oxidizes quinine more rapidly than quinidine, but the reverse is true for the enzyme in birds.
11. Pigeon liver has been found to contain no xanthine oxidase, and thus it cannot oxidize hypoxanthine to uric acid.

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APPENDIX A

Abbreviations in this report

ADP	adenosinediphosphate
ADH	alcohol dehydrogenase
AICAR	5-amino-4-imidazole-carboxamide ribotide
AMP	adenosinemonophosphate
ATP	adenosinetriphosphate
ATPase	adenosinetriphosphatase
CoA	coenzyme A
DBA ⁺⁺	10,10'-dimethyl-9,9'-biacridylium ion
dCTP	deoxycysteinetriphosphate
DNA	deoxyribonucleic acid
DPN DPNH	diphosphonucleotide, oxidized and reduced forms (same as NAD and NADH)
dTTP	deoxythyminetriphosphate
FGAM	formylglycinamidine
FGAR	formylglycinamide ribotide
GalNAc	N-acetyl-D-galactosamine
GAR	glycinamide ribotide
GlcNAc	N-acetyl-D-glucosamine
G6P	glucose-6-phosphate
G6Pase	glucose-6-phosphatase
LDH	lactate dehydrogenase
MDH	malate dehydrogenase
NAD NADH	nicotinamide adenine dinucleotide (coenzyme I, also called DPN) oxidized and reduced forms
NADP NADPH	nicotinamide adenine dinucleotide phosphate (coenzyme II, also called TPN) oxidized and reduced forms

PP	pyrophosphate
PRA	phosphoriboxylamide
PRPP	phosphoribose pyrophosphate
RQ	respiratory quotient, defined as the ratio of the volume of O_2 absorbed over some time period
THFA	tetrahydrofolate
TPD	triosephosphate dehydrogenase
UDP	uridinediphosphate
UDPG	uridinediphosphoglucose
UMP	uridinemonophosphate

APPENDIX B

Enzymes cited in this report*
(with recommended nomenclatures and reactions)

Class 1. Oxidoreductases

<u>TRIVIAL NAME</u>	<u>SYSTEMATIC NAME</u>	<u>REACTION</u>
Alcohol dehydrogenase	Alcohol:NAD oxidoreductase	Alcohol + NAD = aldehyde or ketone + reduced NAD
Catalase	Hydrogen-peroxide:hydrogen-peroxide oxidoreductase	$H_2O_2 + H_2O_2 = O_2 + 2 H_2O$
Cystine reductase	Reduced-NAD:L-cystine oxidoreductase	Reduced NAD + L-cystine = NAD + 2 L-cysteine
Cytochrome <u>c</u> reductase	Reduced-NAD:(acceptor) oxidoreductase	Reduced NAD + acceptor = NAD + reduced acceptor
Cytochrome oxidase	Ferrocyclochrome <u>c</u> :oxygen oxidoreductase	$4 \text{ Ferrocyclochrome } \underline{c} + O_2 = 4 \text{ ferricycyclochrome } \underline{c} + 2 H_2O$
Dihydrofolate dehydrogenase	7,8-Dihydrofolate:NADP oxidoreductase	7,8-Dihydrofolate + NADP = folate + reduced NADP
Folic acid reductase	5,6,7,8-Tetrahydrofolate NADP oxidoreductase	5,6,7,8-Tetrahydrofolate + NADP = 7,8-dihydrofolate + reduced NADP
Glucose dehydrogenases	β -D-Glucose:NAD(P) oxidoreductase	β -D-Glucose + NAD(P) = D-glucono- δ -lactone + reduced NAD(P)
Glucose-6-phosphate dehydrogenase	D-Glucose-6-phosphate:NADP oxidoreductase	D-Glucose 6-phosphate + NADP = D-glucono- δ -lactone 6-phosphate + reduced NADP
Glucuronolactone reductase	L-Gulono- γ -lactone:NADP oxidoreductase	L-Gulono- γ -lactone + NADP = D-glucurono- γ -lactone + reduced NADP
Glutamate dehydrogenase	L-Glutamate:NAD oxidoreductase (deaminating)	L-Glutamate + H_2O + NAD = 2-oxoglutarate + NH_3 + reduced NAD

*The systematic names and reactions are given according to the 1964 recommendations, Report of Commission on Enzymes, International Union of Biochemistry. The trivial names are those of the authors.

<u>TRIVIAL NAME</u>	<u>SYSTEMATIC NAME</u>	<u>REACTION</u>
Glutathione dehydrogenase	Glutathione:dehydro-ascorbate oxidoreductase	2 Glutathione + dehydro-ascorbate = oxidized glutathione + ascorbate
Glutathione peroxidase	Glutathione:hydrogen-peroxide oxidoreductase	2 Glutathione + H ₂ O ₂ = oxidized glutathione + 2 H ₂ O
Glycerol-3-phosphate dehydrogenase	L-Glycerol-3-phosphate: NAD oxidoreductase	L-Glycerol 3-phosphate + NAD = dihydroxyacetone phosphate + reduced NAD
Glycerolphosphate dehydrogenase	L-Glycerol-3-phosphate: (acceptor) oxidoreductase	L-Glycerol 3-phosphate + acceptor = dihydroxyacetone phosphate + reduced acceptor
3-Hydroxybutyrate dehydrogenase	D-3-Hydroxybutyrate: NAD oxidoreductase	D-3-Hydroxybutyrate + NAD = acetoacetate + reduced NAD
Isocitrate dehydrogenase	<u>threo</u> -D ₅ -Isocitrate: NAD oxidoreductase	<u>threo</u> -D ₅ -Isocitrate + NAD = 2-oxoglutarate + CO ₂ + reduced NAD
Lactate dehydrogenase	L-Lactate: NAD oxidoreductase	L-Lactate + NAD = pyruvate + reduced NAD
Malate dehydrogenase	L-Malate: NAD oxidoreductase	L-Malate + NAD = oxaloacetate + reduced NAD
Malate oxidase	L-Malate: oxygen	L-Malate + O ₂ = oxaloacetate + (?)
Monoamine oxidase	Monoamine: oxygen oxidoreductase (deaminating)	A monoamine + H ₂ O + O ₂ = an aldehyde + NH ₃ + H ₂ O ₂
Oestradiol 17-β-dehydrogenase	Oestradiol: NAD 17-β-oxidoreductase	Oestradiol + NAD = oestrone + reduced NAD
Phosphogluconate dehydrogenase	6-Phospho-D-gluconate: NAD(P) oxidoreductase (Decarboxylating)	6-Phospho-D-gluconate + NAD(P) = 6-phospho-2-keto-D-gluconate + reduced NAD(P)
Succinate dehydrogenase	Succinate: (acceptor) oxidoreductase	Succinate + acceptor = fumarate + reduced acceptor
Triosephosphate dehydrogenase	D-Glyceraldehyde-3-phosphate: NADP oxidoreductase	D-Glyceraldehyde 3-phosphate + NADP + H ₂ O = 3-phospho-D-glycerate + reduced NADP
Tryptophan pyrrolase	L-Tryptophan: oxygen oxidoreductase	L-Tryptophan + O ₂ = L-formylkynurenine
Uricase	Urate: oxygen oxidoreductase	Urate + O ₂ = unidentified products

<u>TRIVIAL NAME</u>	<u>SYSTEMATIC NAME</u>	<u>REACTION</u>
Xanthine oxidase	Xanthine:oxygen oxidoreductase	Xanthine + H ₂ O + O ₂ = urate + H ₂ O ₂
Class 2. Transferases		
5-Amino-4-imidazole-carboxamide ribotide		AICAR + 10-formyl-THFA = Formyl-AICAR + THFA
	L-arginine:glycine amidino-transferase	
Carnitine acetyltransferase	Acetyl-CoA:carnitine <u>O</u> -acetyltransferase	Acetyl-CoA + carnitine = CoA + <u>O</u> -acetylcarnitine
Catechol methyltransferase	<u>S</u> -Adenosylmethionine:catechol <u>O</u> -methyltransferase	<u>S</u> -Adenosylmethionine + catechol = <u>S</u> -adenosylhomocysteine + guaiacol
Choline acetylase	Acetyl-CoA:choline <u>O</u> -acetyltransferase	Acetyl-CoA + choline = CoA + <u>O</u> -acetylcholine
Creatine kinase	ATP:creatine phosphotransferase	ATP + creatine = ADP + phosphocreatine
Formylglycinamide ribotide amido-transferase		FGAR + L-glutamine + ATP + H ₂ O = FGAM + L-glutamic acid + ADP + Pi
α -Glucan phosphorylase	α -1,4-Glucan:orthophosphate glucosyltransferase	(α -1,4-Glucosyl) _n + orthophosphate = (α -1,4-glucosyl) _{n-1} + α -D-glucose 1-phosphate
Glutamic-oxaloacetic transaminase	L-Aspartate:2-oxoglutarate aminotransferase	L-Aspartate + 2-oxoglutarate = oxaloacetate + L-glutamate
Glutamic-pyruvic transaminase	L-Alanine:2-oxoglutarate aminotransferase	L-Alanine + 2-oxoglutarate = pyruvate + L-glutamate
Glycinamide ribotide transformylase		GAR + 5,10-methylene-THFA + H ₂ O = FGAR + THFA + H ⁺
Hexokinase	ATP:D-hexose 6-phosphotransferase	ATP + D-hexose = ADP + D-hexose 6-phosphate
Myokinase	ATP:AMP phosphotransferase	ATP + AMP = ADP + ADP
NAD kinase	ATP:NAD 2'-phosphotransferase	ATP + NAD = ADP + NADP
Ornithine carbamoyl-transferase	Carbamoylphosphate:L-ornithine carbamoyl-transferase	Carbamoylphosphate + L-ornithine = orthophosphate + L-citrulline

<u>TRIVIAL NAME</u>	<u>SYSTEMATIC NAME</u>	<u>REACTION</u>
Phosphoglucomutase	α -D-Glucose-1,6-diphosphate: α -D-glucose-1-phosphate phosphotransferase	α -D-glucose 1,6-diphosphate + α -D-glucose 1-phosphate = α -D-glucose 6-phosphate + α -D-glucose 1,6-diphosphate
Phosphoglycerate mutase	2,3-Diphospho-D-glycerate:2-phospho-D-glycerate phosphotransferase	2,3-Diphospho-D-glycerate + 2-phospho-D-glycerate = 3-phospho-D-glycerate + 2,3-diphospho-D-glycerate
Phosphoribosylpyrophosphate amidotransferase	Ribosylamine-5-phosphate:pyrophosphate phosphoribosyltransferase (glutamate-amidating)	β -Ribosylamine 5-phosphate + pyrophosphate + L-glutamate = L-glutamine + 5-phospho- α -D-ribosepyrophosphate + H ₂ O
5-Phosphoribosylpyrophosphate amidotransferase		PRPP + L-glutamine + H ₂ O = PRA + L-glutamic acid + PP
Tyrosine-pyruvate aminotransferase	L-Tyrosine:pyruvate aminotransferase	L-Tyrosine + pyruvate = p-hydroxyphenylpyruvate + L-alanine
UDPglucose-glycogen glucosyltransferase	UDPglucose:glycogen α -4-glucosyltransferase	UDPglucose + (glycogen) _n = UDP + (glycogen) _{n+1}
Class 3. Hydrolases		
Acetylcholinesterase	Acetylcholine hydrolase	Acetylcholine + H ₂ O = choline + acetate
Acid phosphatase	Orthophosphoric monoester phosphohydrolase	An orthophosphoric monoester + H ₂ O = an alcohol + orthophosphate
Adenosine deaminase	Adenosine aminohydrolase	Adenosine + H ₂ O = inosine + NH ₃
Aliesterase	Carboxylic-ester hydrolase	A carboxylic ester + H ₂ O = an alcohol + a carboxylate
Alkaline phosphatase	Orthophosphoric monoester phosphohydrolase	An orthophosphoric monoester + H ₂ O = an alcohol + orthophosphate
AMP deaminase	AMP aminohydrolase	AMP + H ₂ O = IMP + NH ₃
α -Amylase	α -1,4-Glucan 4-glucanohydrolase	Hydrolyses α -1,4-glucan links in polysaccharides containing three or more α -1,4-linked D-glucose units

<u>TRIVIAL NAME</u>	<u>SYSTEMATIC NAME</u>	<u>REACTION</u>
Apyrase	ATP diphosphohydrolase	$ATP + H_2O = ADP + \text{ortho-phosphate}$
Arginase	L-Arginine amidinohydrolase	$L\text{-Arginine} + H_2O = L\text{-ornithine} + \text{urea}$
ATPase	ATP phosphohydrolase	$ATP + H_2O = ADP + \text{ortho-phosphate}$
ATPase	ATP pyrophosphohydrolase	$ATP + H_2O = AMP + \text{pyrophosphate}$
Carboxypeptidase A	Peptidyl-L-amino-acid hydrolase	$A \text{ peptidyl-L-amino acid} + H_2O = \text{a peptide} + \text{an L-amino acid}$
Chymotrypsin A		Hydrolyses peptides, amides, esters, etc., especially at bonds involving the carboxyl groups of aromatic L-amino acids
Chymotrypsin B		Specificity similar to chymotrypsin A
Deoxyribonuclease I	Deoxyribonucleate oligonucleotidohydrolase	$DNA + (n-1)H_2O = n \text{ oligodeoxyribonucleotides} + 5'\text{-monophosphates}$
Deoxyribonuclease II	Deoxyribonucleate 3'-nucleotidohydrolase	Forms 3'-nucleotides and 3'-monophosphates from DNA
Elastase		Hydrolyses peptides, especially at bonds adjacent to neutral amino acid residues
Formylase	Aryl-formylamine amidohydrolase	$\underline{N}\text{-Formyl-L-kynurenine} + H_2O = \text{formate} + L\text{-kynurenine}$
Glucose-6-phosphatase	D-Glucose-6-phosphate phosphohydrolase	$D\text{-Glucose 6-phosphate} + H_2O = D\text{-glucose} + \text{orthophosphate}$
β -Glucuronidase	β -D-Glucuronide glucuronohydrolase	$\beta\text{-D-glucuronide} + H_2O = \text{an alcohol} + D\text{-glucuronate}$
Inorganic pyrophosphatase	Pyrophosphate phosphohydrolase	$\text{Pyrophosphate} + H_2O = 2 \text{ orthophosphate}$
Invertase	β -D-Fructofuranoside fructohydrolase	$A \beta\text{-D-fructofuranoside} + H_2O = \text{an alcohol} + D\text{-fructose}$
Lactase	β -D-Galactoside galactohydrolase	$A \beta\text{-D-galactoside} + H_2O = \text{an alcohol} + D\text{-galactose}$

<u>TRIVIAL NAME</u>	<u>SYSTEMATIC NAME</u>	<u>REACTION</u>
Lipase	Glycerol-ester hydrolase	A triglyceride + H ₂ O = a diglyceride + a fatty acid ion
5'-Nucleotidase	5'-Ribonucleotide phospho-hydrolase	A 5'-ribonucleotide + H ₂ O = a ribonucleoside + ortho-phosphate
Pepsin		Hydrolyses peptides, including those with bonds adjacent to aromatic or dicarboxylic L-amino acid residues
Pepsin B		Hydrolyses peptides; the specificity is similar to that of pepsin
Phosphodiesterase	Orthophosphoric diester phosphohydrolase	A phosphoric diester + H ₂ O = a phosphoric monoester + an alcohol
Phosphoprotein phosphatase	Phosphoprotein phospho-hydrolase	A phosphoprotein + n H ₂ O = a protein + n orthophosphate
Phytase	<u>meso</u> -Inositol-hexaphosphate phosphohydrolase	<u>meso</u> -Inositol hexaphosphate + 6 H ₂ O = <u>meso</u> -inositol + 6 orthophosphate
Pseudo-cholinesterase	Acylcholine acyl-hydrolase	An acylcholine + H ₂ O = choline + an anion
Trypsin		Hydrolyses peptides, amides, esters, etc., at bonds involving the carboxyl groups of L-arginine or L-lysine

Class 4. Lyases

Aconitate hydratase	Citrate (isocitrate) hydro-lyase	Citrate = <u>cis</u> -aconitate + H ₂ O
Aldolase	Ketose-1-phosphate aldehyde-lyase	A ketose 1-phosphate = dihydroxyacetone phosphate + an aldehyde
5-Amino-4-imidazole-N-succinocarboxamide ribotide cleavage enzyme		Succino-AICAR = AICAR + fumaric acid
5-Aminoimidazole ribotide carboxylase		AIR + CO ₂ = CAIR
Carbonic anhydrase	Carbonate hydro-lyase	H ₂ CO ₃ (or H ⁺ + HCO ₃ ⁻) = CO ₂ + H ₂ O

<u>TRIVIAL NAME</u>	<u>SYSTEMATIC NAME</u>	<u>REACTION</u>
Citrate-cleavage enzyme	ATP:citrate oxaloacetate-lyase (CoA-acetylating and ATP-dephosphorylating)	ATP + citrate + CoA = ADP + orthophosphate + acetyl-CoA + oxaloacetate
Cysteine synthetase	L-Serine hydro-lyase (adding hydrogen sulphide)	L-Serine + H ₂ S = L-cysteine + H ₂ O
Enolase	2-Phospho-D-glycerate hydro-lyase	2-Phospho-D-glycerate = phospho-enolpyruvate + H ₂ O
Fumarate hydratase	L-Malate hydro-lyase	L-Malate = fumarate + H ₂ O
Hydroxytryptophan	5-Hydroxy-L-tryptophan carboxy-lyase	5-Hydroxy-L-tryptophan = 5-hydroxytryptamine + CO ₂
Inosinicase		Formyl-AICAR = IMP + H ₂ O
Oxaloacetate decarboxylase	Oxaloacetate carboxy-lyase	Oxaloacetate = pyruvate + CO ₂
D-Serine dehydratase	D-Serine hydro-lyase (deaminating)	D-Serine + H ₂ O = pyruvate + NH ₃ + H ₂ O

Class 5. Isomerases

Methylmalonyl-CoA mutase	Methylmalonyl-CoA CoA-carboxylmutase	Methylmalonyl-CoA = succinyl-CoA
Phosphohexoisomerase	D-Glucose-6-phosphate ketol-isomerase	D-Glucose 6-phosphate = D-fructose 6-phosphate

Class 6. Ligases

Acetyl-CoA carboxylase	Acetyl-CoA:carbon-dioxide ligase (ADP)	ATP + acetyl-CoA + CO ₂ + H ₂ O = ADP + orthophosphate + malonyl-CoA
5-Amino-4-imidazole-N-succinocarboxamide ribotide kinosynthase		CAIR + L-aspartic acid + ATP = succino-AICAR + ADP + Pi
Formylglycinamidine ribotide kinocyclodehydrose		FGAM + ATP = AIR + ADP + Pi
Glutamine synthetase	L-Glutamate:ammonia ligase (ADP)	ATP + L-glutamate + NH ₃ = ADP + orthophosphate + L-glutamine
Glycinamide ribotide kinosynthase		Glycine + ATP + PRA = GAR + ADP + Pi
Pyruvate carboxylase	Pyruvate:carbon-dioxide ligase (ADP)	ATP + pyruvate + CO ₂ + H ₂ O = ADP + orthophosphate + oxaloacetate

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