Title: Myology and Serology of the Avian Family Fringillidae: A Taxonomic Study

Author: William B. Stallcup

Release Date: October 19, 2010 [EBook #33914]

Language: English

Credits: Produced by Chris Curnow, Tom Cosmas, Joseph Cooper and the Online Distributed Proofreading Team at http://www.pgdp.net

Transcriber's Notes

Except for the typographical correction noted below and a few minor changes (missing/extra punctuation) which may have been made but not noted here, the text is the same as presented in the original publication. Some text has been rearranged to restore paragraphs that were split by tables or images. Most of the illustrations have notation to denote the scale compared to the original specimen (example: × 3). Due to the variation in monitor resolution and geometry, the scale is most likely not correct; but is provided as a guide.

Typographical Corrections

Page 187, Table 1 Item 5 : Intavenous => Intravenous

[Cover]

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Volume 8, No. 2, pp. 157-211, figures 1-23, 4 tables

November 15, 1954

Myology and Serology of the Avian Family Fringillidae, A Taxonomic Study

BY

WILLIAM B. STALLCUP

UNIVERSITY OF KANSAS
LAWRENCE
1954

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Volume 8, No. 2, pp. 157-211, figures 1-23, 4 tables

November 15, 1954

Myology and Serology of the Avian Family Fringillidae, A Taxonomic Study

BY

WILLIAM B. STALLCUP

UNIVERSITY OF KANSAS
LAWRENCE
1954

UNIVERSITY OF KANSAS PUBLICATIONS, MUSEUM OF NATURAL HISTORY

[Pg 158]

Volume 8, No. 2, pp. 157-211, figures 1-23, 4 tables

Published November 15, 1954

UNIVERSITY OF KANSAS
Lawrence, Kansas

PRINTED BY
FERD VOILAND, JR., STATE PRINTER
TOPEKA, KANSAS
1954

25-4632

[Pg 159]

Myology and Serology of the Avian Family Fringillidae, a Taxonomic Study

BY

WILLIAM B. STALLCUP

CONTENTS

[↑ TOC]

Introduction

The relationships of many groups of birds within the Order Passeriformes are poorly understood. Most ornithologists agree that some of the passerine families of current classifications are artificial groups. These artificial groupings are the result of early work which gave chief attention to readily adaptive external structures. The size and shape of the bill, for example, have been over-emphasized in the past as taxonomic characters. It is now recognized that the bill is a highly adaptive structure and that it frequently shows convergence and parallelism.

Since studies of external morphology have failed in some cases to provide a clear understanding of the relationships of passerine birds, it seems appropriate that attention be given to other morphological features, to physiological features, and to life history studies in an attempt to find other clues to relationships at the family and subfamily levels.

This paper reports the results of a study of the relationships of some birds of the Family Fringillidae and is based on the comparative myology of the pelvic appendage and on the comparative serology of saline-soluble proteins. Where necessary for comparative purposes, birds from other families have been included in these investigations.

It has long been recognized that the Fringillidae include dissimilar groups. Recent work by Beecher (1951b, 1953) on the musculature of the jaw and by Tordoff (1954) primarily on the structure of the bony palate has emphasized the artificial nature of the assemblage although these authors disagree regarding major divisions within it (see below).

The Fringillidae have been distinguished from other families of nine-primaried oscines by only one character—a heavy and conical bill (for crushing seeds). Bills of this form have been developed independently in several other, unrelated, groups; as Tordoff (1954:7) has pointed out, *Molothrus* of the Family Icteridae, *Psittorostra* of the Family Drepaniidae, and most members of the Family Ploceidae have bills as heavy and conical as those of the fringillids. The ploceids are distinguished from the fringillids by a single external character: a fairly well-developed tenth primary whereas in fringillids the tenth primary is absent or vestigial. Tordoff (1954:20) points out, however, that this distinction is of limited value since in other passerine families the tenth primary may be present in some species of a genus and absent in others. The Genus *Vireo* is an example. Furthermore, at least one ploceid (*Philetairus*) has a small, vestigial tenth primary, whereas some fringillids (*Emberizoides*, for example) possess a tenth primary which is rather large and ventrally placed (Chapin, 1917:253-254). Thus, it is obvious that studies based on other features are necessary in order to attain a better understanding of the relationships of the birds involved.

Sushkin's studies (1924, 1925) of the structure of the bony and horny palates have served as a basis for the division of the Fringillidae into as many as five subfamilies (Hellmayr, 1938:v): Richmondeninae, Geospizinae, Fringillinae, Carduelinae, and Emberizinae.

Beecher (1951b:280) points out that "the richmondenine finches arise so uninterruptedly out of the tanagers that ornithologists have had to draw the dividing line between the two groups arbitrarily." His study of pattern of jaw-musculature substantiates this. He states further that the cardueline finches arise without disjunction from the tanagers. He suggests, therefore, that the two groups of "tanager-finches" be made subfamilies of the Thraupidae and that a third subfamily be maintained for the more typical tanagers. He states that the emberizine finches are of different origin, arising from the wood warblers (1953:307). Beecher (1951a:431; 1953:309) includes the Dickcissel, *Spiza americana*, in the Family Icteridae, chiefly on the basis of jaw muscle-pattern and the horny palate.

Tordoff (1954:10-11) presents evidence that the occurrence of palato-maxillary bones in nine-primaried birds indicates relationship among the forms possessing them. He points out that all fringillids except the Carduelinae possess palato-maxillaries that are either free or more or less

fused to the prepalatine bar. He points out also that in all carduelines, the prepalatine bar is flared at its juncture with the premaxilla, and that the mediopalatine processes are fused across the midline; noncardueline fringillids lack these characteristics. In addition to the above he cites differences between the carduelines and the "other" fringillids in the appendicular skeletons, in geographic distribution, in patterns of migration, and in habits. Tordoff concludes, therefore, that the carduelines are not fringillids but ploceids, their closest affinities being with the ploceid Subfamily Estrildinae. On the basis of palatal structure, the Fringillinae and Geospizinae are combined with the Emberizinae, the name Fringillinae being maintained for the subfamily. The tanagers merge with the Richmondeninae on the one hand and with the Fringillinae on the other. On this basis, Tordoff (1954:32) suggests that the Family Fringillidae be divided into subfamilies as follows: Richmondeninae, Thraupinae, and Fringillinae. The carduelines are placed as the Subfamily Carduelinae in the Family Ploceidae. [Pg 162]

From the foregoing, it is apparent that the two most recent lines of research have given rise to conflicting theories regarding relationships within the Family Fringillidae. The purpose of my investigation, therefore, has been to gather information, from other fields, which might clarify the relationships of these birds.

Since the muscle pattern of the leg in the Order Passeriformes is thought to be one of long standing and slow change, any variation which consistently distinguishes one group of species from another could be significant. With the hope that such variation might be found, a study of the comparative myology of the legs was undertaken.

The usefulness of comparative serology as a means of determining relationship has been demonstrated in many investigations. Its use in this instance was undertaken for several reasons: comparative serology has its basis in biochemical systems which seem to evolve slowly; its methods are objective; and its use has, heretofore, resulted in the accumulation of data which seem compatible, in most instances, with data obtained from other sources.

I acknowledge with pleasure the guidance received in this study from Prof. Harrison B. Tordoff of the University of Kansas. I am indebted also to Prof. Charles A. Leone without whose direction and assistance the serological investigations would not have been possible; to Professors E. Raymond Hall and A. Byron Leonard whose suggestions and criticisms have been most helpful in the preparation of this paper; and to T. D. Burleigh of the U. S. Fish and Wildlife Service for gifts of several specimens used in this work. Assistance with certain parts of the study were received from a contract (NR163014) between the Office of Naval Research of the United States Navy and the University of Kansas.

Myology of the Pelvic Appendage

[↑ TOC]

General Statement

In an excellent paper in which the muscles of the pelvic appendage of birds are carefully and accurately described, Hudson (1937) reviewed briefly the more important literature pertaining to the musculature of the leg which had been published to that date. A review of such information here, therefore, seems unnecessary.

Myological formulae suggested by Garrod (1873, 1874) have been extensively used by taxonomists as aids in characterizing the orders of birds. Relatively few investigations, however, involving the comparative myology of the leg have been undertaken at family and subfamily levels. The works of Fisher (1946), Hudson (1948), and Berger (1952) are notable exceptions. [Pg 163]

The terminology for the muscles used in this paper follows that of Hudson (1937), except that I have followed Berger (1952) in Latinizing all names. Homologies are not given since these are reviewed by Hudson. Osteological terms are from Howard (1929).

Materials and Methods

[↑ TOC]

Specimens were preserved in a solution of one part formalin to eight parts of water. Thorough injection of all tissues was necessary for satisfactory preservation. Most of the down and contour feathers were removed to allow the preservative to reach the skin.

In preparing specimens for study, the legs and pelvic girdle were removed and washed in running water for several hours to remove much of the formalin. They were then transferred to a mixture of 50 per cent alcohol and a small amount of glycerine.

All specimens were dissected with the aid of a low power binocular microscope. Where possible, several specimens of each species were examined for individual differences. Such differences were found to be slight, involving mainly size and shape of the muscles. The size is

dependent partly on the age of the bird, muscles from older birds being larger and better developed. The shape of a muscle (whether long and slender or short and thick) is due in part to the position in which the leg was preserved; that is to say, a muscle may be extended in one bird and contracted in another. For these reasons, descriptions and comparisons are based mainly on the origin and insertion of a muscle and on its position in relation to adjoining muscles.

Birds dissected in this study are listed below (in the order of the A. O. U. Check-List):

SPECIES

Vireo olivaceus (Linnaeus)
Seiurus motacilla (Vieillot)
Passer domesticus (Linnaeus)
Estrilda amandava (Linnaeus)
Poephila guttata (Reichenbach)
Icterus galbula (Linnaeus)
Molothrus ater (Boddaert)
Piranga rubra (Linnaeus)
Richmondena cardinalis (Linnaeus)
Guiraca caerulea (Linnaeus)
Passerina cyanea (Linnaeus)
Spiza americana (Gmelin)
Hesperiphona vespertina (Cooper)
Carpodacus purpureus (Gmelin)
Pinicola enucleator (Linnaeus)
Leucosticte tephrocotis (Swainson)
Spinus tristis (Linnaeus)
Loxia curvirostra Linnaeus
Chlorura chlorura (Audubon)
Pipilo erythrophthalmus (Linnaeus)
Calamospiza melanocorys Stejneger
Chondestes grammacus (Say)
Junco hyemalis (Linnaeus)
Spizella arborea (Wilson)
Zonotrichia querula (Nuttall)
Passerella iliaca (Merrem)
Calcarius lapponicus (Linnaeus)

[↑ TOC]

Description of Muscles

The descriptions which follow are those of the muscles in the leg of the Red-eyed Towhee, *Pipilo erythrophthalmus*. Differences between species, where present, are noted for each muscle. The term thigh is used to refer to the proximal segment of the leg; the term crus is used for that segment of the leg immediately distal to the thigh.

Musculus iliotrochantericus posticus (Fig. 2).—The origin of this muscle is fleshy from the entire concave lateral surface of the ilium anterior to the acetabulum. The fibers converge posteriorly, and the muscle inserts by a short, broad tendon on the lateral surface of the femur immediately distal to the trochanter. It is the largest muscle which passes from the ilium to the femur.

Action.—Moves femur forward and rotates it anteriorly.

Comparison.—No significant differences noted among the species studied.

Musculus iliotrochantericus anticus (Fig. 3).—Covered laterally by the *m. iliotrochantericus posticus*, this slender muscle has a fleshy origin from the anteroventral edge of the ilium between the origins of the *m. sartorius* anteriorly and the *m. iliotrochantericus medius* posteriorly. The *m. iliotrochantericus anticus* is directed caudoventrally and inserts by a broad, flat tendon on the anterolateral surface of the femur between the heads of the *m. femorotibialis externus* and *m. femorotibialis medius* and just distal to the insertion of the *m. iliotrochantericus medius*.

Action.—Moves femur forward and rotates it anteriorly.

Comparison.—No significant differences noted among the species studied.

Musculus iliotrochantericus medius (Fig. 3).—Smallest of the three *iliotrochantericus* muscles, this bandlike muscle has a fleshy origin from the ventral edge of the ilium just posterior to the origin of the *m. iliotrochantericus anticus*. The fibers are directed caudoventrally, and the insertion is tendinous on the anterolateral surface of the femur between the insertion of the other two *iliotrochantericus* muscles.

Action.—Moves femur forward and rotates it anteriorly.

Comparison.—No significant differences noted among the species studied.

Musculus iliacus (Figs. 4, 5).—Arising from a fleshy origin on the ventral edge of the ilium just posterior to the origin of the *m. iliotrochantericus medius*, this small slender muscle passes posteroventrally to its fleshy insertion on the posteromedial surface of the femur just proximal to the origin of the *m. femorotibialis internus*.

Action.—Moves femur forward and rotates it posteriorly.

Comparison.—No significant differences among the species studied.

Musculus sartorius (Figs. 1, 4).—A long, straplike muscle, the *sartorius* forms the anterior edge of the thigh. The origin is fleshy, half from the anterior edge of the ilium and from the median dorsal ridge of this bone and half from the posterior one or two free dorsal vertebrae. The insertion is fleshy along a narrow line on the anteromedial edge of the head of the tibia and on the medial region of the patellar tendon.

Action.—Moves thigh forward and upward and extends shank.

Comparison.—In *Loxia* and *Spinus*, only one-third of the origin is from the last free dorsal vertebra. In *Hesperiphona*, *Carpodacus*, *Pinicola*, and *Leucosticte*, only one-fifth of the origin is from this vertebra.

Musculus iliotibialis (Fig. 1).—Broad and triangular, this muscle covers most of the deeper [Pg 165] muscles of the lateral aspect of the thigh. The middle region is fused with the underlying *femorotibialis* muscles. In the distal half of this muscle there are three distinct parts; the anterior and posterior edges are fleshy and the central part is aponeurotic. The origin is from a narrow line along the iliac crests—from the origin of the *m. sartorius*, anteriorly, to the origin of the *m. semitendinosus* posteriorly. The origin is aponeurotic in the preacetabular region but fleshy in the postacetabular region. The distal part of the muscle is aponeurotic and joins with the *femorotibialis* muscles in the formation of the patellar tendon. This tendon incloses the patella and inserts on a line along the proximal edges of the cnemial crests of the tibiotarsus.

Action.—Extends crus.

Comparison.—In *Vireo* the central aponeurotic portion of this muscle is absent.

Musculus femorotibialis externus (Fig. 2).—Covering the lateral and anterolateral surfaces of the femur, this large muscle has a fleshy origin from the lateral edge of the proximal three-fourths of the femur. The origin separates the insertion of the *m. iliotrochantericus anticus* from that of the *m. ischiofemoralis* and, in turn, is separated from the origin of the *m. femorotibialis medius* by the insertions of the *m. iliotrochantericus anticus* and *m. iliotrochantericus medius*. Approximately midway of the length of the femur this muscle fuses anteromesially with the *m. femorotibialis medius*. Distally, the *m. femorotibialis externus* contributes to the formation of the patellar tendon which inserts on a line along the proximal edges of the cnemial crests of the tibiotarsus.

Action.—Extends crus.

Comparison.—No significant differences noted among the species studied.

Musculus femorotibialis medius (Figs. 2, 4).—The origin of this muscle, which lies along the anterior edge of the femur, is fleshy from the entire length of the femur proximal to the level of attachment of the proximal arm of the biceps loop. Laterally this muscle is completely fused for most of its length with the *m. femorotibialis externus* and contributes to the formation of the patellar tendon, which inserts on a line along the proximal edges of the cnemial crests of the tibiotarsus. Many of the fibers, nevertheless, insert on the proximal edge of the patella.

Action.—Extends crus.

Comparison.—No significant differences noted among the species studied.

Musculus femorotibialis internus (Fig. 4).—One of the most superficial muscles lying on the medial surface of the thigh, this muscle is divided, especially near the distal end, into two parts, lateral and medial. The origin of the lateral part is fleshy from a line on the medial surface of the femur; the origin begins proximally at a point near the insertion of the *m. iliacus*. The medial, bulkier part of the muscle has a fleshy origin on the medial surface of the lower one-third of the femur. The two parts fuse to some extent above the points of insertion and insert on the medial edge of the head of the tibia.

Action.—Rotates tibia anteriorly.

Comparison.—Two parts of this muscle variously fused; otherwise, no significant differences in the species studied.

Musculus piriformis (Fig. 3).—This muscle is represented by the *pars caudifemoralis* only, the *pars iliofemoralis* being absent in passerine birds as far as is known. The *pars caudifemoralis* is flat, somewhat spindle-shaped, and passes anteroventrally from the pygostyle to the femur. The origin is tendinous from the anteroventral edge of the pygostyle, and the insertion is semitendinous on the posterolateral surface of the shaft of the femur about one-fourth its length from the proximal end. [Pg 166]

Action.—Moves femur posteriorly and rotates it in this direction; moves tail laterally and depresses it.

Comparison.—No significant differences noted among the species studied.

Musculus semitendinosus (Figs. 2, 3, 5).—The origin from the extreme posterior edge of the posterior iliac crest of the ilium is fleshy and is aponeurotic from the last vertebra of the synsacrum and the transverse processes of several caudal vertebrae. The straplike belly passes along the posterolateral margin of the thigh. Immediately posterior to the knee, the muscle is divided transversely by a ligament. That portion passing anteriorly from the ligament is the *m. accessorius semitendinosi* (here considered a part of the *m. semitendinosus*) and is discussed below. The ligament continues distally in two parts; one part inserts on the medial surface of the *pars media* of the *m. gastrocnemius* and the other part fuses with the tendon of insertion of the *m. semimembranosus*.

The *m. accessorius semitendinosi* extends anteriorly from the above mentioned ligament to a fleshy insertion on the posterolateral surface of the femur immediately proximal to the condyles.

Action.—Moves femur posteriorly, flexes the crus and aids in extending the tarsometatarsus.

Comparison.—No significant differences noted among the species studied.

Musculus semimembranosus (Figs. 3, 4, 5).—This straplike muscle passes along the posteromedial surface of the thigh. The origin is semitendinous along a line on the ischium, from a point dorsal to the middle of the ischiopubic fenestra to the posterior end of the ischium, and from a small area of the abdominal musculature posterior to the ischium. The insertion is by means of a broad, thin tendon on a ridge on the medial surface of the tibia immediately distal to the head of this bone. The tendon of insertion passes between the head of the *pars media* and *pars interna* of the *m. gastrocnemius* and is fused with the tendon of the *m. semitendinosus*.

Action.—Flexes crus.

Comparison.—No significant differences noted among the species studied.

Musculus biceps femoris (Fig. 2).—Long, thin, and somewhat triangular, this muscle lies on the lateral side of the thigh just underneath the *m. iliotibialis*. Its origin is from a line along the anterior and posterior iliac crests underneath the origin of the *m. iliotibialis*. Anterior to the acetabulum the origin is aponeurotic, and the edge of this aponeurosis passes over the proximal end of the femur. The origin posterior to the acetabulum is fleshy. The most anterior point of origin is difficult to ascertain but it lies near the center of the anterior iliac crest. The most posterior point of origin is immediately dorsal to the posterior end of the ilioischiatic fenestra. Behind the knee the fibers of this muscle converge to form the strong tendon of insertion which passes through the biceps loop, under the tendon of origin of the *m. flexor perforatus digiti II*, and inserts on a small tubercle on the posterolateral edge of the fibula at the point of the tibia-fibula fusion. [Pg 167]

The biceps loop is tendinous and the distal end attaches to a protuberance on the posterolateral edge of the femur at the proximal edge of the external condyle. The proximal end attaches to the anterolateral edge of the femur immediately proximal to the distal end of the loop, which extends posterior to the femur. The distal arm of this loop is connected with the tendon of origin of the *m. flexor perforatus digiti II* by a strong tendon.

Action.—Flexes crus.

Comparison.—No significant differences noted among the species studied.

Musculus ischiofemoralis (Fig. 3).—Short and thick, this muscle arises directly from the lateral surface of the ischium between the posterior iliac crest and the ischiopubic fenestra. The area of origin extends to the posterior edge of the ischium. The insertion is tendinous on the lateral surface of the trochanter opposite the insertion of the *m. iliotrochantericus medius*.

Action.—Moves femur posteriorly and rotates it in this direction.

Comparison.—No significant differences noted among the species studied.

Musculus obturator internus (Figs. 4, 7).—Lying on the inside of the pelvis and covering the medial surface of the ischiopubic fenestra, is this flat, pinnate, leaf-shaped muscle. The origin is fleshy and is from the ischium and pubis around the edges of this fenestra; none of the fibers arises from the membrane stretched across the fenestra. Anteriorly the fibers converge and form a strong tendon that passes through the obturator foramen and inserts on the posterolateral surface of the trochanter of the femur.

Action.—Rotates femur posteriorly.

Comparison.—No significant differences noted among the species studied.

Musculus obturator externus (Fig. 7).—Short and fleshy, this muscle consists of two parts which are not easily separable but which may be traced throughout its length. The parts are more nearly distinct at the origin. The dorsal part arises directly from the ischium along the dorsal edge of the obturator foramen. The larger ventral part arises directly from the anterior and ventral edges of the obturator foramen. The fibers of the dorsal part pass anteriorly, cover the tendon of the *m. obturator internus* laterally, and insert on the trochanter around the point of insertion of the latter muscle. The fibers of the ventral part pass parallel with the tendon of the *m. obturator internus* and insert on the trochanter immediately distal and posterior to the tendon of the latter muscle.

Action.—Rotates femur posteriorly.

Comparison.—In *Passer*, *Estrilda*, *Poephila*, *Hesperiphona*, *Carpodacus*, *Pinicola*, *Leucosticte*, *Spinus* and *Loxia*, this muscle is undivided and, in its position, origin, and insertion, resembles the ventral part of the bipartite muscle described above. The origin is from the anterior and ventral edges of the obturator foramen and the insertion is on the trochanter of the femur immediately distal and posterior to the insertion of the *m. obturator internus*. In all other genera examined, the muscle is bipartite. In *Chlorura* the dorsal part is larger and better developed than it is in the other genera.

Musculus adductor longus et brevis (Figs. 3, 4, 5).—Consisting of two distinct, straplike parts, this large muscle lies on the medial surface of the thigh, posterior to the femur.

The *pars anticus* has a semitendinous origin on a line that extends posteriorly from the posteroventral edge of the obturator foramen to a point half way across the membrane that covers the ischiopubic fenestra. The insertion is fleshy along the posterior surface of the femur from the level of the insertion of the *m. piriformis* distally to the medial surface of the internal condyle. [Pg 168]

The *pars posticus* originates by a broad, flat tendon on a line across the posterior half of the membrane that covers the ischiopubic fenestra. The insertion is at the point of origin of the *pars media* of the *m. gastrocnemius* on the posteromedial surface of the proximal end of the internal condyle of the femur. There is a broad tendinous connection with the proximal end of the *pars media* of the *m. gastrocnemius*. The anterior edge of the *pars posticus* is overlapped medially by the posterior edge of the *pars anticus*.

Action.—Flexes thigh; may flex crus also and may extend tarsometatarsus.

Comparison.—In *Vireo olivaceous*, the origin of this muscle does not extend the length of the ischiopubic fenestra. The origin, furthermore, is along the dorsal edge of the ischiopubic fenestra and not from the membrane covering the fenestra. Finally, in this species, the origin of the *pars posticus* is fleshy.

Musculus tibialis anticus (Figs. 2, 5).—Lying along the anterior edge of the crus, a part of this muscle is covered by the *m. peroneus longus*. The origin is by two distinct heads, each of which is pinnate. The anterior head arises directly from the edges of the outer and inner cnemial crests. The posterior head arises by a short, strong tendon from a small pit on the anterodistal edge of the external condyle of the femur. This tendon and the proximal end of the muscle pass between the head of the fibula and the outer cnemial crest. The two heads of the muscle fuse at a place slightly more than one-half of the distance down the crus. At the distal end of the crus this muscle gives rise to a strong tendon which passes under a fibrous loop immediately proximal to

the external condyle in company with the *m. extensor digitorum longus* and which passes between the condyles of the tibia and inserts on a tubercle on the anteromedial edge of the proximal end of the tarsometatarsus.

Action.—Flexes tarsometatarsus.

Comparison.—No significant differences noted among the species studied.

Musculus extensor digitorum longus (Figs. 3, 5, 8).—Slender and pinnate, this muscle lies along the anteromedial surface of the tibia. The origin is fleshy from most of the region between the cnemial crests and from a line along the anterior surface of the proximal fourth of the tibia. Approximately two-thirds of the distance down the crus the muscle gives rise to the tendon of insertion which passes through the fibrous loop near the distal end of the tibia in company with the *m. tibialis anticus*. The tendon then passes along beneath the supratendinal bridge at the distal end of the tibia, traverses the anterior intercondylar fossa, and passes beneath a bony bridge on the anteromedial surface of the proximal end of the tarsometatarsus. The tendon continues along the anterior surface of the tarsometatarsus to a point immediately above the bases of the toes and there gives rise to three branches, one to the anterior surface of each foretoe. The insertions of each branch are on the anterior surfaces of the phalanges as shown in Fig. 8.

Action.—Extends foretoes.

Comparison.—This muscle is weakly developed in *Leucosticte* and *Calvarius*; the belly is slender and extends only half way down the crus before giving rise to the tendon of insertion. The [Pg 169] functional significance of this variation is difficult to understand. The convergence in muscle pattern shown by these two genera, however, is in all probability the result of similarities in behavior patterns. These birds perch less frequently than do the other birds studied. Thus, the toes are neither flexed nor extended as often; the smaller size of the *m. extensor digitorum longus* may have resulted in part from this lessened activity. Except for the variations just noted, there are no significant differences among the species studied; even the rather complex patterns of insertion are identical.

Musculus peroneus longus (Fig. 1).—Relatively thin and straplike, this muscle lies on the anterolateral surface of the crus and is intimately attached to the underlying muscles. The part of the origin from the proximal edges of the inner and outer cnemial crests is semitendinous but the part of the origin from the lateral edge of the shaft of the fibula is tendinous. Approximately two-thirds the distance down the crus the muscle gives rise to the tendon of insertion. Immediately above the external condyle of the tibiotarsus this tendon divides. The posterior branch inserts on the proximal end of the lateral edge of the tibial cartilage. The anterior branch passes over the lateral surface of the external condyle to the posterior surface of the tarsometatarsus and there unites with the tendon of the *m. flexor perforatus digiti III*.

Action.—Extends tarsometatarsus and flexes third digit.

Comparison.—No significant differences noted among the species studied.

Musculus peroneus brevis (Figs. 2, 3).—Lying along the anterolateral surface of the tibia, this slender, pinnate muscle arises from a fleshy origin along this surface and along the anterior surface of the fibula from a point immediately proximal to the insertion of the *m. biceps femoris* to a point approximately two-thirds of the way down the crus. Near the distal end of the tibia the muscle gives rise to the tendon of insertion that passes through a groove on the anterolateral edge of the tibia just above the external condyle. Here the tendon is held in place by a broad fibrous loop and passes under the anterior branch of the tendon of insertion of the *m. peroneus longus* and inserts on a prominence on the lateral edge of the proximal end of the tarsometatarsus.

Action.—Extends tarsometatarsus and may abduct it slightly.

Comparison.—No significant differences noted among the species studied.

Musculus gastrocnemius (Figs. 1, 4).—The largest muscle of the pelvic appendage, it covers superficially all of the posterior surface, most of the medial surface, and half of the lateral surface of the crus. The muscle originates by three distinct heads.

The *pars externa* covers the posterolateral surface of the crus, is intermediate in size between the other two heads, and arises by a short, strong tendon from a small bony protuberance on the posterolateral side of the distal end of the femur immediately proximal to the fibular condyle. The tendon is intimately connected with the distal arm of the loop for the *m. biceps femoris*.

The *pars media* is the smallest of the three heads and lies on the medial surface of the crus. The head of the *pars media* is separated from the *pars interna* by the tendon of insertion of the *m. semimembranosus* and originates by a short, strong tendon from the posteromedial surface of the proximal end of the internal condyle of the femur. The proximal portion of the *pars media* has tendinous connections with the tendon of the *m. semitendinosus* and with the *pars posticus* of the *m. adductor longus et brevis*.

The *pars interna* is the largest of the three heads and covers most of the medial surface of the crus. This head in its proximal portion is distinctly divided into anterior and posterior parts, the former overlapping the latter medially. The origin of the posterior part is fleshy from the anterior half of the tibial head. Some of the fibers of the anterior part arise directly from the inner cnemial crest while its remaining fibers arise from the patellar tendon (Fig. 1) and form a band that extends around the anterior surface of the knee, covering the insertion of the *m. sartorius*. [Pg 170]

Approximately half way down the crus, the three heads give rise to the tendon of insertion, the *tendo achillis*, which passes over and is tightly bound to the posterior surface of the tibial cartilage. The insertion is tendinous on the posterior surface of the hypotarsus and along the posterolateral ridge of the tarsometatarsus. This tendon seems to be continuous with a fascia which forms a sheath around the posterior surface of the tarsometatarsus holding the other tendons of this region firmly in the posterior sulcus.

Action.—Extends tarsometatarsus.

Comparison.—Study of the *pars externa* and *pars media* reveals no significant differences among the species dissected. The *pars interna*, however, is subject to some variation which is described below.

Pars interna bipartite

Vireo	*Chlorura*
Seiurus	*Pipilo*
Icterus	*Calamospiza*
Molothrus	*Chondestes*
Piranga	*Junco*
Richmondena	*Spizella*
Guiraca	*Zonotrichia*
Passerina	*Passerella*
Spiza	*Calcarius*

The two parts of the *m. gastrocnemius* are most distinct in *Vireo*. *Icterus*, *Molothrus*, *Richmondena*, *Guiraca*, and *Passerina* lack the fibrous band that passes around the front of the knee. In *Spiza* this band of fibers is smaller than in the other species.

Pars interna undivided

Passer	*Pinicola*
Estrilda	*Leucosticte*
Poephila	*Spinus*
Hesperiphona	*Loxia*
Carpodacus	

In *Leucosticte*, although the *pars interna* is undivided, there is a band of fibers which extends around the front of the knee (see discussion, p. 183).

Musculus plantaris (Fig. 5).—Small and slender, this muscle lies on the posteromedial surface of the crus, beneath the *pars interna* of the *m. gastrocnemius* and originates by fleshy fibers from the posteromedial surface of the proximal end of the tibia immediately distal to the internal articular surface. The belly extends approximately one-sixth of the way down the crus and gives rise to a long, slender tendon that inserts on the proximomedial edge of the tibial cartilage. [Pg 171]

Action.—Extends tarsometatarsus.

Comparison.—No significant differences noted among the species studied.

Musculus flexor perforatus digiti II (Figs. 3, 9).—This is a slender muscle which lies on the lateral side of the crus beneath the *pars externa* of the *m. gastrocnemius* and is intimately connected anteromedially with the *m. flexor digitorum longus* and posteromedially with the *m. flexor hallucis longus*. The origin is by a strong tendon from the lateral surface of the external condyle of the femur at the point of origin of the *m. flexor perforans et perforatus digiti II*. This

tendon serves also as the origin of the anterior head of the *m. flexor hallucis longus*. The tendon connects also by a broad tendinous band with the distal arm of the loop for the *m. biceps femoris* and by a similar band with the lateral edge of the fibula immediately distal to the head. The tendon of insertion passes distally, perforates the tibial cartilage near its lateral edge, traverses the middle medial canal of the hypotarsus (Fig. 6), and passes distally to the foot. At the distal end of the tarsometatarsus the tendon is held against the medial surface of the first metatarsal by a straplike sheath. The tendon then passes over a sesamoid bone between the first metatarsal and the base of the second digit and is bound to this bone by a sheath. The tendon inserts mainly along the posteromedial edge of the proximal end of the first phalanx of the second digit, although the termination is sheathlike and covers the entire posterior surface of this phalanx. This sheathlike termination is perforated by the tendons of the *m. flexor perforans et perforatus digiti II* and the branch of the *m. flexor digitorum longus* that inserts on the second digit.

Action.—Flexes second digit.

Comparison.—In *Vireo* this muscle is larger and more deeply situated than it is in the other species examined and has no connection with the *m. flexor hallucis longus*.

Musculus flexor perforatus digiti III (Fig. 5).—Long and flattened, this muscle lies on the posteromedial side of the crus beneath the *m. gastrocnemius*. The belly is tightly fused laterally with the belly of the *m. flexor hallucis longus* and posteriorly with the belly of the *m. flexor perforatus digiti IV*. The origin is by a long, strong tendon from a small tubercle just medial to, and at the proximal end of, the external condyle of the femur. Below the middle of the crus this muscle terminates in a strong tendon which perforates the tibial cartilage near its lateral edge. In this region the tendon is sheathlike and wrapped around the tendon of the *m. flexor perforatus digiti IV*. These two tendons together pass through the posterolateral canal of the hypotarsus (Fig. 6). Immediately distal to the hypotarsus the two tendons separate, and the tendon of the *m. flexor perforatus digiti III* receives a branch of the tendon of the *m. peroneus longus*. The tendon passes distally over the surface of the second trochlea, and its insertion is sheathlike on the posterior surface of the first phalanx, and on the proximal end of the second. In the area of insertion this tendon is perforated by that of the *m. flexor perforans et perforatus digiti III* and by that of the *m. flexor digitorum longus* to the third digit.

Action.—Flexes digit III.

Comparison.—In *Passer*, *Estrilda*, *Poephila*, *Hesperiphona*, *Carpodacus*, *Pinicola*, *Leucosticte*, *Spinus*, and *Loxia* the edges of the sheathlike tendon are thickened at the points of insertion, so that the tendon appears to have two branches which insert along the posterolateral edges of the first phalanx and are connected medially by a fascia.

Musculus flexor perforatus digiti IV (Fig. 3).—Extending along the posterior edge of the crus, this slender muscle lies beneath the *m. gastrocnemius*. The belly is fused with those of the *m. flexor hallucis longus* and *m. flexor perforatus digiti III*. Its origin is fleshy from the intercondyloid region of the distal end of the femur and has a few fibers arising from the tendon of origin of the *m. flexor perforatus digiti III*. Near the distal end of the crus the muscle gives rise to the strong tendon of insertion which perforates the tibial cartilage near its lateral edge and in this region is ensheathed by the tendon of the *m. flexor perforatus digiti III*. The two tendons pass together through the posterolateral canal of the hypotarsus (Fig. 6). The tendon continues distally along the tarsometatarsus and the posterior surface of digit IV. The tendon bifurcates at approximately the middle of the first phalanx. A short lateral branch inserts on the posterolateral edge of the proximal end of the second phalanx. The long medial branch is perforated by a branch of the *m. flexor digitorum longus*; the distal end is flattened, has thickened edges, and inserts over the posterior surfaces of the distal end of the second phalanx, and over the proximal end of the third phalanx.

Action.—Flexes digit IV.

Comparison.—No significant differences noted among the species studied.

Musculus flexor perforans et perforatus digiti II (Figs. 2, 9).—Small and spindle-shaped, this muscle lies on the posterolateral side of the crus immediately beneath the *pars externa* of the *m. gastrocnemius*. The origin is fleshy and arises in company with the *m. flexor perforans et perforatus digiti III* from a point on the posterolateral surface of the distal end of the femur between the point of origin of the *pars externa* of the *m. gastrocnemius* and the fibular condyle. The belly extends approximately one-fourth of the way down the crus and gives rise to the tendon of insertion which passes distally and superficially through the posterior edge of the tibial cartilage. The tendon traverses the posteromedial canal of the hypotarsus (Fig. 6) and continues along the posterior surface of the tarsometatarsus. Between the first metatarsal and the base of the second digit the tendon is enclosed by the medial surface of a sesamoid bone. This tendon then perforates that of the *m. flexor perforatus digiti II* at the level of the first phalanx and in

turn is perforated by the tendon of the *m. flexor digitorum longus* at the proximal end of the second phalanx. The insertion is on the posterior surface of the second phalanx.

Action.—Flexes digit II.

Comparison.—In *Passer*, *Estrilda*, *Poephila*, *Hesperiphona*, *Carpodacus*, *Pinicola*, *Leucosticte*, *Spinus*, and *Loxia* the proximal portion of this muscle is more intimately connected with the posterior edge of the *m. flexor perforans et perforatus digiti III* than it is in the other species examined.

Musculus flexor perforans et perforatus digiti III (Fig. 2).—Long and pinnate, this muscle lies on the lateral surface of the crus beneath the *m. peroneus longus* and *pars externa* of the *m. gastrocnemius*. There are two distinct heads. The origin of the anterior head is fleshy from the proximal edge of the outer cnemial crest and from the internal edge of the distal end of the patellar tendon. The posterior head arises by a tendon from the femur in company with the *m. flexor perforans et perforatus digiti II*, is connected also with the tendon of origin of the *m. flexor perforatus digiti II*, and is loosely attached to the head of the fibula. Fibers from the belly of the muscle attach throughout its length to the lateral edge of the fibula, and the muscle is tightly [Pg 173] fused also with adjacent muscles. The tendon of insertion is formed approximately one-half the way down the crus. The tendon perforates the posterior surface of the tibial cartilage and passes through the posteromedial canal of the hypotarsus (Fig. 6). At the base of the third digit the tendon ensheathes that of the *m. flexor digitorum longus* and the two together perforate the tendon of the *m. flexor perforatus digiti III*. Immediately distal to this perforation the tendon of the *m. flexor perforans et perforatus digiti III* ceases to ensheath that of the *m. flexor digitorum longus*. The latter passes beneath that of the former. Near the distal end of the second phalanx the tendon of the *m. flexor digitorum longus* perforates that of the *m. flexor perforans et perforatus digiti III*. The latter inserts on the posterior surface of the distal end of the second phalanx and the proximal end of the third.

Action.—Flexes digit III.

Comparison.—In *Passer*, *Estrilda*, and *Poephila*, and in all the cardueline finches examined the proximal portion of this muscle is more intimately connected with the anterior edge of the *m. flexor perforans et perforatus digiti II* than it is in the other species examined.

Musculus flexor digitorum longus (Figs. 3, 5).—This strong, pinnate muscle is deeply situated along the posterior surfaces of the tibia and fibula. There are two distinct heads of origin. The lateral head arises by means of fleshy fibers from the posterior edge of the head of the fibula. The medial head arises by means of fleshy fibers from the region under the ledgelike external and internal articular surfaces of the proximal end of the tibia. Neither head has any connection with the femur in contrast to the condition, described by Hudson (1937: 46-47) in the crow, *Corvus brachyrhynchos*, and in the raven, *Corvus corax*. Near the point of insertion of the *m. biceps femoris* the two heads fuse. The common belly is attached by fleshy fibers to the posterior surface of the tibia and fibula for two-thirds of the distance down the crus. Near the distal end of the crus the muscle terminates in a strong tendon which passes deeply through the tibial cartilage and traverses the anteromedial canal of the hypotarsus (Fig. 6). About midway down the tarsometatarsus this tendon becomes ossified. Immediately above the bases of the toes it gives rise to three branches, one to the posterior surface of each of the foretoes. These branches perforate the other flexor muscles of the toes as described in the accounts of those muscles and insert as follows: The branch to digit II inserts on the base of the ungual phalanx and by a stout, tendinous slip on the distal end of the second phalanx (Fig. 9). The branch to digit III inserts on the base of the distal end of the third phalanx and a stronger slip to the distal end of the second or proximal end of the third. The branch to digit IV inserts on the base of the ungual phalanx, with one tendinous slip to the distal end of the third phalanx and another to the distal end of the fourth.

Action.—Flexes foretoes.

Comparison.—No significant differences noted among the species studied.

Musculus flexor hallucis longus (Fig. 3).—Situated immediately posterior to the *m. flexor digitorum longus*, the belly of this large, pinnate muscle is intimately connected anteriorly to that of the *m. flexor perforatus digiti II*. The *m. flexor hallucis longus* arises by two heads which are separated by the tendon of insertion of the *m. biceps femoris*. The smaller anterior head arises from the same tendon as does the *m. flexor perforatus digiti II*. The larger posterior head arises [Pg 174] by means of fleshy fibers from the intercondyloid region of the posterior surface of the femur along with the *m. flexor perforatus digiti III* and *IV*. The two heads join just distal to the point of insertion of the *m. biceps femoris*. There is no trace of a tendinous band connecting the two heads as there is in the crow and in the raven (Hudson, 1937:49). Near the distal end of the shank the muscle gives rise to a strong tendon which perforates the tibial cartilage along its

lateral edge and passes through the anterolateral canal of the hypotarsus (Fig. 6). The tendon crosses over to the medial surface of the tarsometatarsus, passes distally, and perforates the sheathlike tendon of the *m. flexor hallucis brevis* between the first metatarsal and the trochlea for digit II. The tendon continues along the posterior surface of the hallux and has a double insertion; the main tendon attaches to the base of the ungual phalanx and a smaller branch inserts on the distal end of the proximal phalanx.

Action.—Flexes hallux.

Comparison.—In *Vireo* this muscle has only the posterior head of origin and is not connected with the *m. flexor perforatus digiti II*. The muscle is proportionately smaller and weaker than in any of the other species studied.

Musculus extensor hallucis longus (Fig. 4).—One of the smallest muscles of the leg, the origin is fleshy from the anteromedial edge of the proximal end of the tarsometatarsus. The belly is long and slender and terminates distally in a slender tendon which passes distally along the posterior surfaces of the first metatarsal and the first digit. The insertion is on the base of the ungual phalanx. Near the distal end of the proximal phalanx, the tendon passes between two thick bands of fibro-elastic tissue which insert also on the ungual phalanx. These bands of tissue function as automatic extensors of the claw.

Action.—Extends hallux; action must be slight.

Comparison.—In *Vireo* this muscle is proportionately larger and better developed than it is in any of the other species examined.

Musculus flexor hallucis brevis (Fig. 4).—This minute muscle has a fleshy origin from the medial surface of the hypotarsus. The short belly terminates in a weak, slender tendon which passes down the posteromedial surface of the tarsometatarsus and into the space between the first metatarsal and the trochlea for digit II. In this region the tendon envelops the tendon of the *m. flexor hallucis longus* and inserts on the distal end of the first metatarsal and on the proximal end of the first phalanx of the first digit.

Action.—Flexes hallux; action must be slight.

Comparison.—The small size of this muscle makes it exceedingly difficult to study. The muscle is larger in *Vireo* than in any of the other species examined. This may be correlated with the smaller size of the *m. flexor hallucis longus* in this species. The muscle does not seem to be so well developed in the cardueline finches as it is in the other species.

Musculus abductor digiti IV (Fig. 2).—Extremely small, delicate and difficult to demonstrate, this muscle arises in a fleshy origin immediately from underneath the posterior edge of the external cotyla of the tarsometatarsus. The tendon of insertion is long and slender and inserts along the lateral edge of the first phalanx of digit IV.

Action.—Abducts digit IV. [Pg 175]

Comparison.—No significant differences noted among the species studied.

Musculus lumbricalis.—Semitendinous throughout its length, this muscle arises from the ossified tendon of the *m. flexor digitorum longus* at a point immediately proximal to the branching of this tendon. The insertion is on the joint pulleys and capsules at the base of the third and fourth digits.

Action.—Hudson (1937:57) states that: "Meckel (*vide* Gadow—1891, p. 204) considered this muscle as serving to draw the joint pulley behind in order to protect it from pinching during the bending of the toes. It perhaps also tends to flex the third and fourth digits."

Comparison.—No significant differences noted among the species studied.

Discussion of the Myological Investigations

[↑ TOC]

Simpson (1944:12) and others have emphasized that different parts of organisms evolve at different rates. Beecher (1951b:275) in stating that "... the hind limb is very similar in muscle pattern throughout the Order Passeriformes and seems to have become relatively static after attaining a high level of general efficiency ..." implies that the muscle pattern of the leg must be one of long standing and slow change. This concept was emphasized by Hudson (1937) who

found but little variation in muscle pattern among members of the several families of passerine birds. The concept is further confirmed by the present investigation. The intricate patterns of origin and of insertion seem to remain almost the same throughout the order in spite of adaptive radiation which has occurred.

Two major differences in patterns of leg-musculature, however, were found among the species studied, and these differences are significant since they are consistent between subfamilies. The muscles involved are the *m. obturator externus* and the *pars interna* of the *m. gastrocnemius*.

The *m. obturator externus* is bipartite, consisting of dorsal and ventral parts, in the passerine species studied by Hudson (1937) and in all of the species examined by me except the ploceids and the cardueline finches. In the ploceids and cardueline finches this muscle is undivided and resembles in its position, origin, and insertion only the ventral portion of the muscle found in the other birds studied. It is difficult to imagine what advantage or disadvantage might be associated with the bipartite or with the undivided condition. The action of this muscle is to rotate the femur (right femur clockwise, left femur counterclockwise), and certainly the greater mass of the bipartite muscle could lend greater strength to such action. The possible significance of this is discussed below.

List of Abbreviations Used in Figures

Abd. dig. IV

M. abductor digiti IV

Acc.

M. accessorius semitendinosi

Add. long.

M. adductor longus et brevis

Anterolat. can. Anterolateral canal of hypotarsus

Anteromed. can. Anteromedial canal of hypotarsus

Bic. fem.

M. biceps femoris

Bic. loop Loop for

m. biceps femoris

Ext. cot. External cotyla

Ext. dig. l.

M. extensor digitorum longus

Ext. hal. l.

M. extensor hallucis longus

Fem. tib. ext.

M. femorotibialis externus

Fem. tib. int.

M. femorotibialis internus

Fem. tib. med.

M. femorotibialis medius

F. dig. l.

M. flexor digitorum longus

F. hal. brev.

M. flexor hallucis brevis

F. hal. l.

M. flexor hallucis longus

F. p. et p. d. II

M. flexor perforans et perforatus digiti II

F. p. et p. d. III

M. flexor perforans et perforatus digiti III

F. per. d. II

M. flexor perforatus digiti II

F. per. d. III

M. flexor perforatus digiti III

F. per. d. IV

M. flexor perforatus digiti IV

Gas.

M. gastrocnemius

Iliacus

M. iliacus

Il. tib.

M. iliotibialis

Il. troc. ant.

M. iliotrochantericus anticus

Il. troc. med.

M. iliotrochantericus medius

Il. troc. post.

M. iliotrochantericus posticus

Int. cot. Internal cotyla

Isch. fem.

M. ischiofemoralis

Midmed. can. Midmedial canal of hypotarsus

Obt. ext.

M. obturator externus

Obt. int.

M. obturator internus

P. ant.

Pars anticus

P. ext.

Pars externa

P. int.

Pars interna

P. med.

Pars media

P. post.

Pars posticus

Per. brev.

M. peroneus brevis

Per. long.

M. peroneus longus

Pirif.

M. piriformis

Plan.

M. plantaris

Posterolat. can. Posterolateral canal of hypotarsus

Posteromed. can. Posteromedial canal of hypotarsus

Sar.

M. sartorius

Semim.

M. semimembranosus

Semit.

M. semitendinosus

Tib. ant.

M. tibialis anticus

Tib. cart. Tibial cartilage

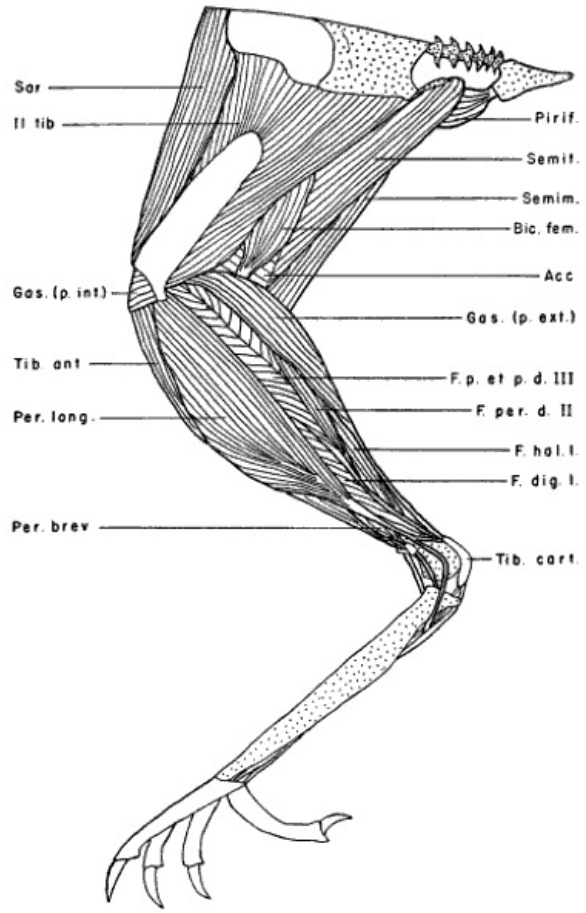


FIG. 1. *Pipilo erythrophthalmus.* Lateral view of the superficial muscles of the left leg, × 1.5.

[Pg 178]

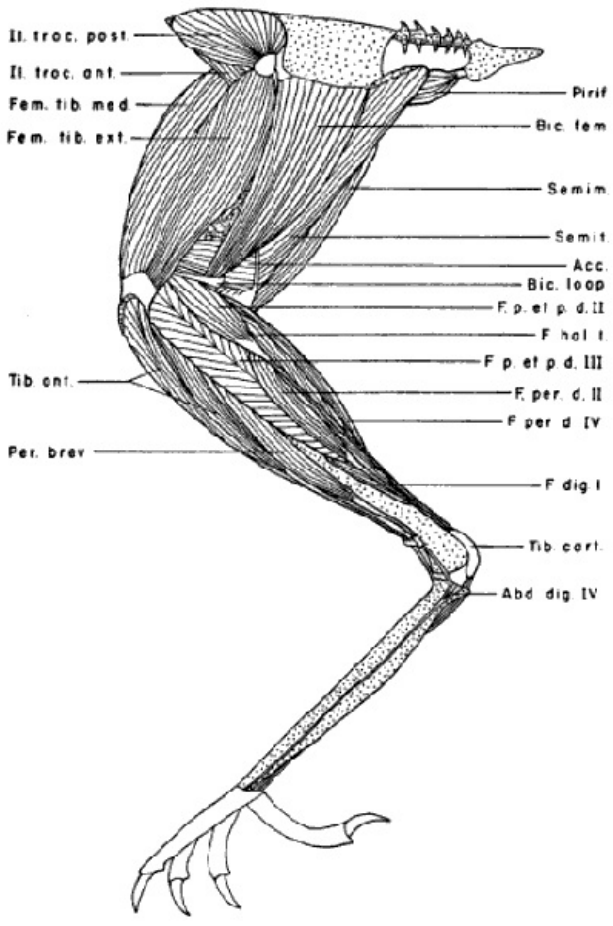


FIG. 2. *Pipilo erythrophthalmus.* Lateral view of the left leg showing a deeper set of muscles. The superficial muscles *iliotibialis*, *sartorius*, *gastrocnemius* and *peroneus longus* have been

removed, × 1.5.

[Pg 179]

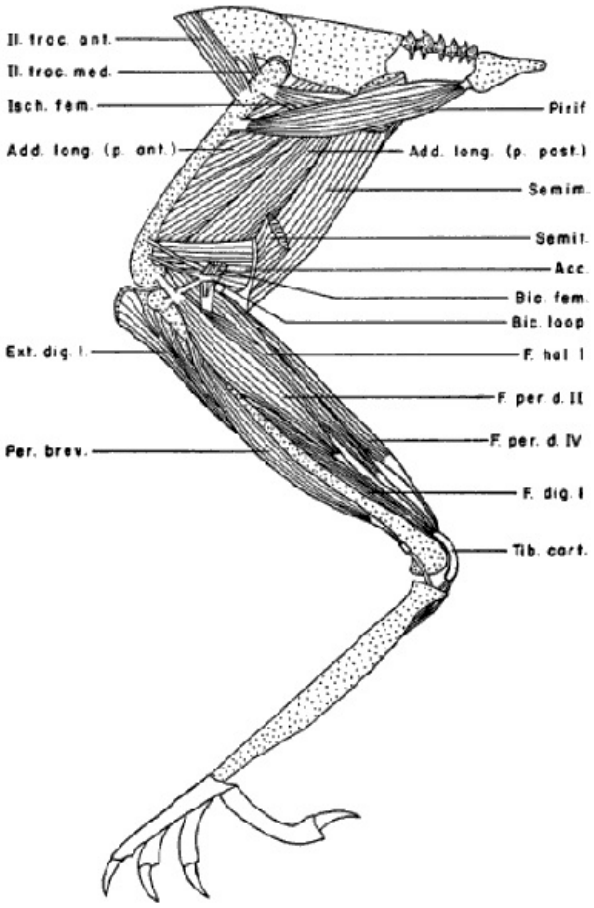


FIG. 3. *Pipilo erythrophthalmus.* Lateral view of the left leg showing the still deeper muscles. In addition to those listed for figure 2, the following muscles have been wholly or partly removed: *iliotrochantericus posticus*, *femorotibialis externus*, *femorotibialis medius*, *biceps femoris*, *semitendinosus*, *tibialis anticus*, *flexor perforans et perforatus digiti II*, and *flexor perforans et perforatus digiti III*, × 1.5.

[Pg 180]

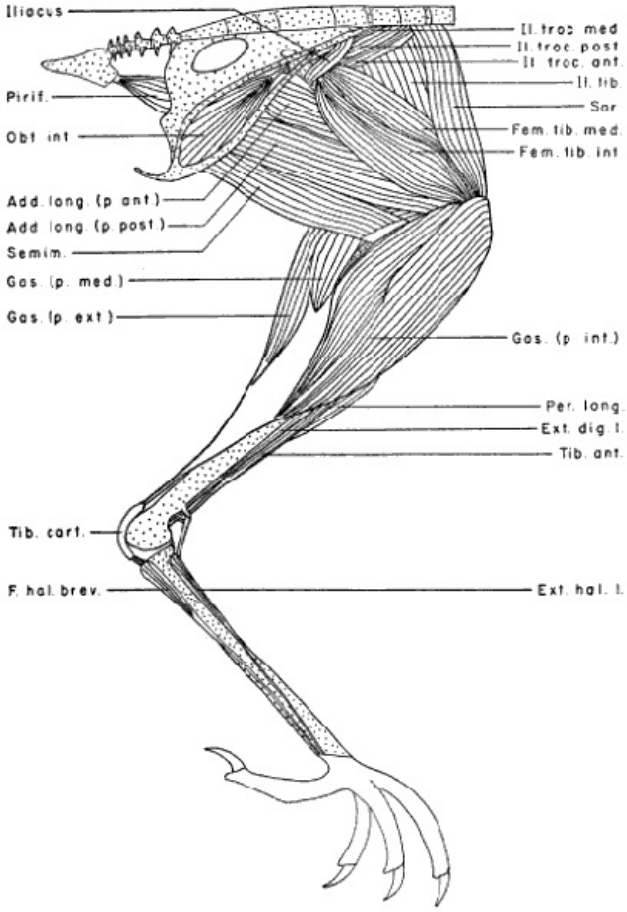


FIG. 4. *Pipilo erythrophthalmus.* Medial view of the superficial muscles of the left leg, × 1.5.

[Pg 181]

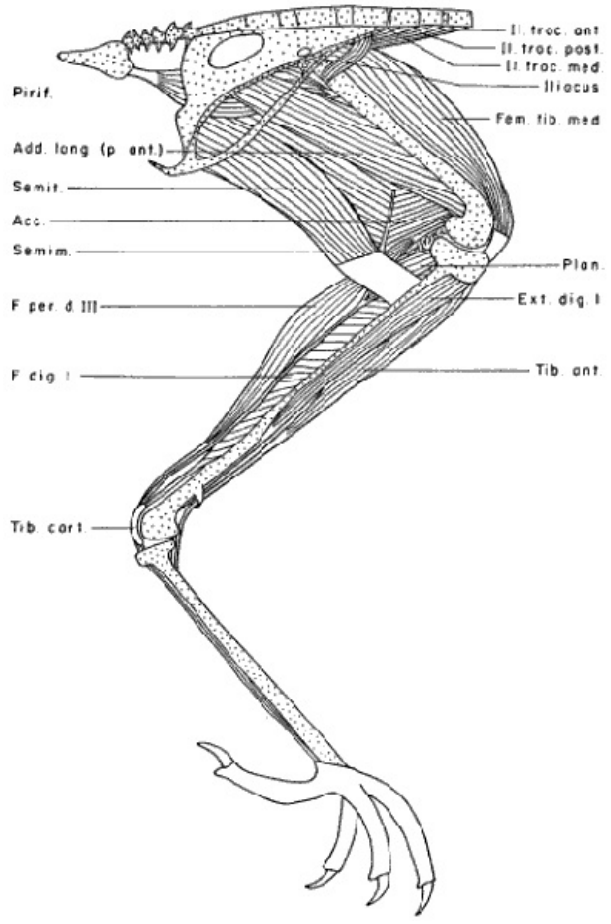


FIG. 5. *Pipilo erythrophthalmus.* Medial view of the left leg showing a deeper set of muscles than those seen in figure 4. The following superficial muscles have been removed: *iliotibialis,*

sartorius, *femorotibialis internus*, *obturator internus*, *adductor longus (pars posticus)*, *gastrocnemius*, and *peroneus longus*, × 1.5.

[Pg 182]

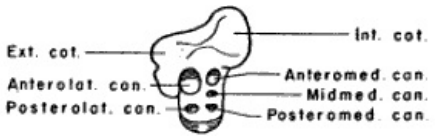


Figure 6

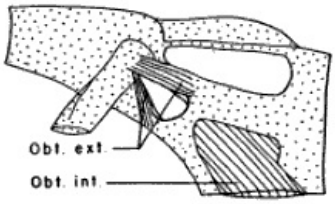


Figure 7

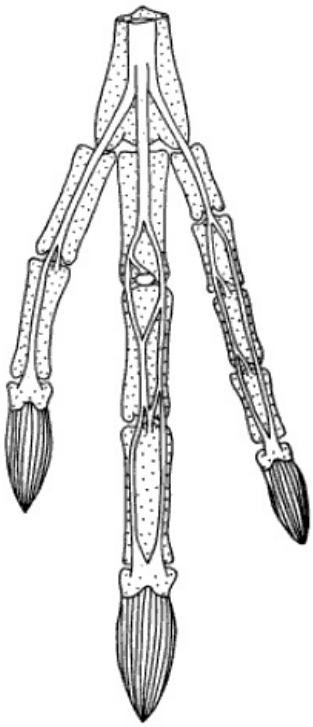


Figure 8

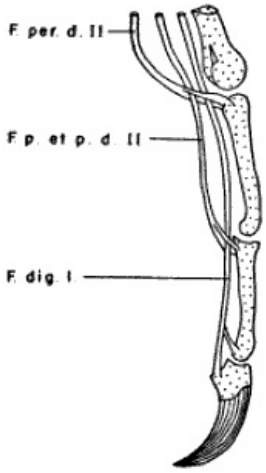


Figure 9

FIG. 6. *Pipilo erythrophthalmus.* Proximal end of left tarsometatarsus and the hypotarsus, × 4.

FIG. 7. *Pipilo erythrophthalmus.* Lateral view of proximal end of left femur and a portion of the pelvis, × 3.5.

FIG. 8. *Pipilo erythrophthalmus.* Upper surfaces of the phalanges of the foretoes of the left foot showing insertions of the *M. extensor digitorum longus*, × 3.

FIG. 9. *Pipilo erythrophthalmus.* Medial view of the second digit of the left foot, showing insertions of the flexor muscles, × 3.

[Pg 183]

The division of the *pars interna* of the *m. gastrocnemius* into anterior and posterior parts has not been reported by previous authors yet the division is quite distinct in those birds in which it occurs. Hudson (1937:36) points out that in some non-passerine birds the *pars interna* is double, but that in these species the *m. semimembranosus* inserts between the two parts. This is not the condition in those species studied by me. Only the ploceids and the cardueline finches in the present investigation fail to show such a division. The undivided muscle in these birds resembles, in its origin and position, the posterior portion of the muscle found in those species showing the bipartite condition. The greater mass of the bipartite muscle probably makes possible a stronger extension of the tarsometatarsus.

Thus, the divided or undivided conditions of the *m. obturator externus* and the *pars interna* of the *m. gastrocnemius* seem to be correlated with the degrees of strength of certain movements of the leg. It is conceivable that these differences in structure are correlated with the manner in which food is obtained, the birds having the bipartite muscles being those which spend the most time on the ground searching and scratching for seeds and other sorts of food. Yet, in

Leucosticte, a cardueline, and in *Calcarius*, an emberizine, whose foraging habits are rather similar, the structure is unlike. *Leucosticte* does resemble the emberizines and also *Piranga* and *Spzia* in the extension of a band of muscle fibers from the *pars interna* of the *m. gastrocnemius* around the front of the knee. A band of muscle fibers of this sort strengthens the knee joint and gives still more strength to the *pars interna*. This condition has been reported in a number of birds by Hudson (1937) and is, in all probability, an adaptation for greater strength of certain leg movements. The development of this band in *Leucosticte* seems to parallel that in the other birds studied and does not indicate relationship, since in *Leucosticte* this band arises from the undivided muscle which (as stated above) resembles only the posterior portion of the bipartite muscle described for the other birds. In the latter, the muscular band arises from the anterior part of the muscle.

Minor differences in muscle pattern, like those already mentioned, are consistent also between subfamilies, but correlation of these minor differences with function is difficult. There is the implication, however, that in all the groups except the carduelines and ploceids, the emphasis is on greater strength and mobility of the leg. In the carduelines that were studied the origin of the *m. sartorius* does not extend so far craniad as in the other species. In the latter, at least half [Pg 184] of the origin is from the last one or two free dorsal vertebrae; in the carduelines no more than one third of the origin is anterior to the ilium. It is conceivable that the more craniad the origin, the stronger the forward movement of the thigh would be.

In *Passer*, *Estrilda* and *Poephila*, and in all the cardueline finches examined, the bellies of the *m. flexor perforans et perforatus digiti II* and the *m. flexor perforans et perforatus digiti III* are more intimately connected than they are in the other species studied. Thus, the amount of independent action of these muscles in *Passer*, in the estrildines, and in the carduelines probably is reduced.

In *Passer*, the estrildines, and the carduelines the edges of the sheathlike tendon of insertion of the *m. perforatus digiti III* are thickened; as a result the insertion appears superficially to be double but closer examination reveals that there is a fascia stretched between the thickened edges. In the other species examined, the insertion is sheathlike throughout and there are no thick areas. I cannot explain this on the basis of function. The difference, however, is obvious and constant.

Aside from the differences noted above, there were variations of muscle pattern that seem to be significant only in *Vireo olivaceus*. In this species the central, aponeurotic portion of the *m. iliotibialis* is absent. The origin of the *m. adductor longus et brevis* is from the dorsal edge of the ischiopubic fenestra and not from the membrane covering this fenestra. The origin of the *pars posticus* of this muscle, furthermore, is fleshy and not tendinous as it is in the other species. The *m. flexor perforatus digiti II* is larger and more deeply situated in *Vireo* and has, furthermore, no connection with the *m. flexor hallucis longus*. The latter muscle is smaller and weaker than in any of the other species and has only one (the posterior) head of origin. The *m. flexor hallucis brevis*, on the contrary, is larger than in the other birds, compensating, probably, for the small *m. flexor hallucis longus*. In those differences, however, which separate the carduelines and ploceids from the other birds studied, *Vireo* resembles, in every instance, the richmondenines, emberizines, tanagers, warblers, and blackbirds.

On the basis of differences in leg-musculature the species which are now included in the Family Fringillidae may be separated into two groups. One group includes the richmondenines and the emberizines; the other, the carduelines. The muscle patterns of the legs of the birds of the first group are indistinguishable from those of *Seiurus*, *Icterus*, *Molothrus*, and *Piranga*, and except for the differences noted are similar to those in *Vireo*. The carduelines, on the other hand, [Pg 185] are similar in every point of leg-musculature to the ploceids which were studied. Thus, the heterogeneity of the Family Fringillidae, as now recognized, is emphasized by differences in the muscle patterns of the leg.

Comparative Serology

[↑ TOC]

General Statement

The application of serological techniques to the problems of animal relationships has been attempted with varying degrees of success over a period of approximately fifty years. Few of the earlier studies were of a quantitative nature, but within the past decade, satisfactory quantitative serological techniques have been developed whereby taxonomic relationships may be estimated. The usefulness of comparative serology in taxonomy has been demonstrated in investigations of many groups wherein results obtained have, in most instances, been compatible with the results obtained by more conventional methods, such as comparative morphology. As Boyden (1942:141) stated, "comparative serology ... is no simple guide to animal relationship." However, the objectiveness of its methods, the fact that it has its basis in the comparisons of biochemical

systems which seem to be relatively slow to change in response to external environmental influences, and the fact that the results are of quantitative nature favor, where possible, the inclusion of data from comparative serology along with that from more conventional sources when an attempt is made to determine the relationships of groups of animals.

The application of serological methods in ornithology has not been extensive. Irwin and Cole (1936) and Cumley and Irwin (1941, 1944) used two species of doves and their hybrids and demonstrated that a distinction between the red cells of these birds could be made by use of immunological methods involving the agglutinin reaction. McGibbon (1945) was able to distinguish the red cells of interspecific hybrids in ducks by similar methods. Irwin (1953) used similar techniques in his study of the evolutionary patterns of some antigenic substances of the blood cells of birds of the Family Columbidae. Sasaki (1928) demonstrated the usefulness of the precipitin technique in distinguishing species of ducks and their hybrids. This technique was used successfully also by DeFalco (1942) and by Martin and Leone (1952). Working with groups of known relationships, these investigators showed that the "accepted" systematic positions of certain birds were confirmed by serological procedures. The precipitin reaction, however, has never been applied to actual problems in avian taxonomy prior to the present study. [Pg 186]

Preparation of Antigens

[↑ TOC]

Although most previous work in comparative serology in which precipitin tests were used has involved the use of whole sera as antigens, Martin and Leone (1952) indicated that tissue extracts are satisfactory as antigens and that serological differentiation can be obtained with these extracts and the antisera to them. I decided, therefore, to use such extracts in these investigations, since the small sizes of the birds to be tested made it impracticable to obtain enough whole sera.

Most of the birds used were obtained by shooting, but a few were trapped and the exotic species were purchased alive from a pet dealer. When a bird was killed, the entire digestive tract was carefully removed to prevent the escape of digestive enzymes into the tissues and to prevent putrefaction by action of intestinal bacteria. As soon as possible (and within three hours in every instance) the bird was skinned, the head, wings, and legs were removed, and the body was frozen. Each specimen, consisting of trunk, heart, lungs, and kidneys, was wrapped separately and carefully in aluminum foil to prevent dehydration of the tissues. The specimens were kept frozen until the time when the extracts were made.

When an extract was to be prepared, the specimen was allowed to thaw but not to become warm. In the cold room with the temperature of all equipment and reagents at 2°C., the specimen was placed in a Waring blender with 0.9 per cent aqueous solution of NaCl buffered with M/150 K_2HPO_4 and M/150 Na_2HPO_4 to a pH of 7.0. The amount of reagent used was 75 ml. of saline for each gram of tissue to be extracted. The tissues were minced in the blender, allowed to stand at 2°C. for 72 hours, and the tissue residues removed by centrifugation in a refrigerated centrifuge. Formalin was added to a portion of the supernatant in the amount necessary to make the final dilution 0.4 per cent. This formolization was found to be necessary to inhibit the action of autolytic enzymes over the period of time required to complete the investigations. The effects of formolization on the antigenicity and reactivity of proteins are discussed later. It was necessary to sterilize and clarify the "native" (unformolized) extracts; this was done by filtration through a Seitz filter. These "native" substances were used only in the early stages of the investigation (see below). The filtrate was bottled and stored at 2°C. In the early stages of this investigation clarification of the formolized extract was accomplished by the same sort of filtration. It was determined, however, that centrifugation in a refrigerated centrifuge at high speeds (17,000g) served the same purpose and was quicker. The formolized extracts were bottled and also stored at 2°C. (although refrigerated storage of the formolized extracts does not seem necessary). For each extract the amount of protein present was determined colorimetrically by the method of Greenberg (1929) with a Leitz Photrometer.

Species for which extracts were prepared and the protein values of the extracts are listed in Table 1. Extracts of some species were used throughout most of the experiment; extracts of others were used only when needed for purposes of comparison.

[Pg 187]

TABLE 1.—SPECIES FROM WHICH EXTRACTS WERE PREPARED AND INJECTION SCHEDULES FOR EXTRACTS AGAINST WHICH ANTISERA WERE PRODUCED

SPECIES	Protein, gms. per 100 ml	Injection schedules for production of antisera
Myiarchus crinitus (Linnaeus)	0.65	Series 1: Intravenous, 0.5, 1.0, 2.0, and 4.0 ml.

Passer domesticus	1.40	Series 1: Subcutaneous, 0.5, 1.0, 2.0, and 4.0 ml.
Estrilda amandava	0.45	[A]Series 1: Intravenous, 0.5, 1.0, 2.0, and 4.0 ml. [A]Series 2: Subcutaneous, 0.5, 1.0, and 2.0 ml. Intraperitoneal, 8.0 ml.
Poephila guttata	0.56	[A]Same as for *Estrilda*.
Molothrus ater	0.65	Series 1: Intravenous and subcutaneous, respectively, 0.5 and 0.5 ml., 1.0 and 1.0 ml., 3.0 and 1.0 ml., 5.0 and 3.0 ml. Series 2: Subcutaneous, 0.5, 1.0, 2.0 and 4.0 ml.
Piranga rubra	0.50	Same as for *Molothrus*.
Richmondena cardinalis	0.70	[A]Same as for *Estrilda*.
Richmondena cardinalis	0.60	Same as for *Spinus*.
Passerina cyanea	0.45	Antiserum not prepared.
Spiza americana	0.70	Same as for *Molothrus*.
Carpodacus purpureus	0.50	Antiserum not prepared.
Spinus tristis	0.49	Series 1: Intravenous, 0.5, 1.0, 2.0, and 4.0 ml. Series 2: Intravenous, 0.5, 1.0, 2.0, and 4.0 ml. Series 3: Subcutaneous, 0.5, 1.0, 2.0, and 4.0 ml.
Pipilo erythrophthalmus	0.92	Antiserum not prepared.
Junco hyemalis	0.56	Same as for *Spinus*.
Spizella arborea	0.48	Same as for *Spinus*.
Zonotrichia querula	0.48	Same as for *Spinus*.
Zonotrichia albicollis (Gmelin)	0.92	Antiserum not prepared.

[A] Antiserum prepared against formolized antigen.

[↑ TOC]

Preparation of Antisera

All antisera were produced in rabbits (laboratory stock of *Oryctolagus cuniculus*). Three methods of injection of antigen were used in various combinations: intravenous, subcutaneous, and intraperitoneal. Injection schedules used in the production of each antiserum are listed in Table 1. Both formolized and "native" antigens were used. Each rabbit received one or more series of four injections, each injection being administered on alternate days and doubling in amount: 0.5 ml., 1.0 ml., 2.0 ml., and 4.0 ml. In all but two instances more than one series of injections was necessary to produce a useful antiserum. More than two series, however, resulted in little or no improvement of the reactivity of the antiserum.

The injection-series were separated by intervals of eight days. On the eighth day after the last injection of each series, 10 ml. of blood were withdrawn from the main artery of the ear of the rabbit, and the antiserum was used in a homologous precipitin test to determine its usefulness. If the antiserum contained sufficient amounts of antibodies to conduct the projected tests, the rabbit was completely exsanguinated by cardiac puncture, by using an 18-gauge needle and a 50 ml. syringe. The whole blood was placed in clean test tubes and allowed to clot. It was allowed to stand at 2°C. for 12 to 18 hours so that most of the serum would be expressed from the clot. The serum was then decanted, centrifuged to remove all blood cells, sterilized in a Seitz filter, bottled in sterile vials, and stored at 2°C. until used.

[↑ TOC]

Methods of Serological Testing

The precipitin reaction is the most successful of the serological techniques thus far devised for systematic comparisons. The reaction occurs because antigenic substances introduced into the body of an animal cause the formation of antibodies which precipitate antigens when the two are mixed. The antisera which are produced show quantitative specificities in their actions; therefore, when an antiserum containing precipitins is mixed with each of several antigens, the reaction involving the homologous antigen (that used in the production of the antiserum) is greater than those reactions involving the heterologous antigens (antigens other than those used in the production of the antiserum). Furthermore, the magnitudes of the reactions between the

antiserum and the heterologous antigens vary according to the degrees of similarity of these antigens to the homologous one.

The method of precipitin testing follows that outlined by Leone (1949). The Libby (1938) Photronreflectometer was used to measure the turbidities developed by the interaction of antigen and antiserum. With this instrument parallel rays of light are passed through the turbid systems being measured. Light rays are reflected from the suspended particles to the sensitive plate of a photoelectric cell; this generates a current of electricity which causes a deflection on a galvanometer. The deflection is proportional to the amount of turbidity developed and readings may be taken directly from the scale of the instrument.

The reaction-cells of the photronreflectometer are designed to operate with a volume of 2 ml.; therefore, this volume was used in all testing. In every series of tests the amount of antiserum was held constant and the amount of antigen was varied. The volume for each antigen dilution was always 1.7 ml., and to this was added 0.3 ml. of antiserum to make up a volume of 2 ml.

TABLE 2.—Percentage values obtained from analyses of precipitin reactions. Numerals represent relative amounts of reaction between antigens and antisera. Homologous reactions are arbitrarily valued as 100 per cent, and heterologous reactions are expressed accordingly. *Comparisons are meaningful only if made within each horizontal row of values.* [Pg 189]

ANTIGENS	ANTISERA							
	Estrilda amandava	*Poephila guttata*	*Piranga rubra*	*Richmondena cardinalis*	*Spiza americana*	*Spinus tristis*	*Junco hyemalis*	*Zonotrichia querula*
Passer domesticus	75	74	73	66	81	72	...	81
Estrilda amandava	100	88	75	...	79	72	53	...
Poephila guttata	95	100	77	67	87	81	...	...
Molothrus ater	66	54	69	65	86	75	69	75
Piranga rubra	...	...	100	...	...	...	...	89
Richmondena cardinalis	75	80	91	100	98	65	88	91
Spiza americana	65	68	...	71	100	64	67	80
Carpodacus purpureus	70	71	71	61	89	93	53	70
Spinus tristis	72	74	73	60	89	100	60	...
Junco hyemalis	64	56	74	65	87	68	100	...
Zonotrichia querula	65	71	...	67	89	75	...	100

Antigens were diluted with 0.9 per cent phosphate-buffered saline solution. Tests were run in standard Kolmer test-tube racks, each test consisting of 12 tubes. Each dilution was made on the basis of the known protein concentration of the antigen. The first tube contained an initial dilution of 1 part protein in 250 parts saline and each successive tube contained a protein dilution one-half the concentration of the preceding tube, ranging up to 1:512,000. Saline controls, antiserum controls, and antigen controls were maintained with each test to determine the turbidities inherent in these solutions. These control-turbidities were deducted from the total turbidity developed in each reaction-tube, the resultant turbidity then being considered as that which was caused by the interaction of antigens and antibodies. The turbidities were allowed to develop over a 24-hour period. In the early stages of this investigation the reactions were allowed to take place at 2°C. in order to inhibit bacterial growth. Later tests were carried out at room temperatures, and bacterial growth was prevented by the addition to each tube of 'Merthiolate' in a final dilution of 1:10,000. [Pg 190]

Experimental Data

[↑ TOC]

Corrected values for the turbidities obtained were plotted with the turbidity values on the ordinate and the antigen dilutions on the abscissa. The homologous reaction was the standard of reference for all other test reactions with the same antiserum. By summing the plotted turbidity readings, numerical values are obtained which are indices serving to characterize the curves.

Such values were converted to percentage values, that of the homologous reaction being considered 100 per cent. These values, plus the curves, provide the data by means of which the proteins of the birds may be compared. Plots representative of the precipitin curves are presented in Figs. 10 to 21. For convenience each plot represents only several of the 10 curves obtained with each antiserum.

A summary of the serological relationships of the birds involved in the precipitin tests is presented in Table 2, in which percentage values are presented. Since the techniques involved in testing were greatly improved as the investigation proceeded, the summary is based solely on those tests run in the later stages of the investigation. For reasons which will become apparent in later discussion, it should be emphasized that in Table 2 comparisons may be made only within each horizontal row of values.

[↑ TOC]

Discussion of the Serological Investigations

One of the problems met early in this investigation was instability of the proteins in the extracts that were prepared. Extracts in which no attempt was made to inactivate the enzymes present proved unsatisfactory. It was necessary to maintain the temperature of the "native" antigens at 2°C, and all work with such antigens had to be performed at this temperature. This arrangement was inconvenient; furthermore, inactivation of the enzymes was not complete even at this low temperature, and some denaturation of the proteins took place as evidenced by the gradual appearance of insoluble precipitates in the stored vials.

The preservatives, 'Merthiolate' and formalin, were used in an attempt to inhibit the autolytic action of the enzymes present. Formalin, when added to make a final dilution of 0.4 per cent, proved to be the more satisfactory of the two preservatives and was used throughout most of the work. Formalin caused slight denaturation of some of the proteins, but this effect was complete within a few hours, after which any denatured material was removed by filtration or centrifugation. The proteins remaining in solution were stable over the period necessary to complete the investigations.

The addition of formalin reduces the reactivity of the extracts when they are tested with antisera prepared against "native" antigens and causes changes in the nature of the precipitin curves. This effect has been pointed out by Horsfall (1934) and by Leone (1953) in their work on the effects of formaldehyde on serum proteins. Their data indicate, however, that even though changes in the immunological characteristics of proteins are brought about by formolization, the proteins retain enough of their specific chemical characteristics to allow consistent differentiation of species by immunological methods. In the tests which I performed, the relative positions of the precipitin curves, whether native or formolized extracts were involved, remained unchanged (Figs. 10, 11). *All data used in interpretation of the serological relationships were obtained from tests in which formolized antigens of equivalent age were used.*

[Pg 191]

Only three antisera were produced against formolized antigens, all others being produced against "native" extracts. The formolized antigens seemed to have a greater antigenicity, in most instances, than did those which were unformolized, and precipitin reactions involving antisera produced against formolized antigens developed higher turbidities. The antisera produced against formolized antigens were equal to but no better than those prepared against "native" extracts in separating the birds tested (Figs. 12, 13).

The rabbit is a variable to be considered in serological tests. Two rabbits exposed to the same antigen, under the same conditions, may produce antisera which differ greatly in their capacities to distinguish different antigens. It is logical to assume, therefore, that two rabbits exposed to different antigens may produce antisera which also differ in this respect. This explains the unequal values of reciprocal tests shown in Table 2. Thus, in the test involving the antiserum to the extracts of *Richmondena*, a value of 71 per cent was obtained for *Spiza* antigen, whereas in the test involving anti-*Spiza* serum, a value of 98 per cent was obtained for *Richmondena* antigen. In Table 2, therefore, comparisons may be made only among values for the proteins of birds tested with the same antiserum.

Since the amount of any one antiserum is limited, there is, of necessity, a limit as to the number of birds used in a series of serological tests. Therefore, although the results reveal the actual serological relationships of the individual species, interpretation of the relationships of the taxonomic groups must be undertaken with the realization that such an interpretation is based on tests involving relatively few species of each group. It is reasonable to assume, however, that a species which has been placed in a group on the basis of resemblances other than serological resemblance would show greater serological correspondence to other members of that group than it would to members of other groups. Specifically, in the Fringillidae and their allies, there seems to be little reason to doubt that genera, and even subfamilies, are natural groups. This is illustrated in tests involving closely related genera: *Richmondena* and *Spiza* (Figs. 14, 15, 18), *Estrilda* and *Poephila* (Fig. 21), *Spinus* and *Carpodacus* (Figs. 12, 17, 19, 20). In each of these tests the pairs of genera mentioned show greater serological correspondence to each other than they do to other kinds involved. This point is illustrated further by a test (not illustrated)

[Pg 192]

involving *Zonotrichia querula* (the homologous antigen) and *Zonotrichia albicollis*. Although this test was one of an earlier series in which difficulties were encountered (the data, therefore, were not used), it is of interest that the two species were almost indistinguishable serologically.

The serological homogeneity of passeriform birds is emphasized by the fact that the value of every heterologous reaction was more than 50 per cent of the value of the homologous reaction, except in the test involving the anti-*Richmondena* serum and *Myiarchus* (Fig. 13) in which the value of the heterologous reaction was 45 per cent. Because most ornithologists consider these genera to be only distantly related (they are in different suborders within the Order Passeriformes), the relatively high value of the heterologous reaction emphasizes the close serological correspondence of passerine birds and indicates that small consistent serological differences among these birds are actually significant. The possibility that some of the serological correspondence is due to the "homologizing" effect of formalin on proteins should not be excluded. I think, however, that this effect is not entirely responsible for the close correspondence observed here.

An additional point to consider in interpretation of the serological tests is that the techniques used tend to separate sharply species that are closely related whereas species that are distantly related are not so easily separated. In other words, comparative serological studies with the photronreflectometer tend to minimize the differences between distant relatives and to exaggerate the differences between close relatives.

In analyzing the serological relationships of the species used in this study, it becomes obvious that two or more series of tests must be considered before the birds can be placed in relation to each other. For example, the data presented in Fig. 14 indicate that *Spiza* and *Molothrus* show approximately the same degree of serological correspondence to *Richmondena*. This does not imply necessarily that *Spiza* and *Molothrus* are closely related. If Fig. 15 is examined, it can be [Pg 193] determined that *Richmondena* shows much greater serological correspondence to *Spiza* than does *Molothrus*. Thus, an analysis of both figures serves to clarify the true serological relationships of the three genera. By reference to other series of tests involving these three birds a more exact determination of their relationships may be obtained.

To illustrate this point by a hypothetical example, two species might seem equidistant, serologically, from a third species. Additional testing should indicate if the first two species are equidistant in the same direction (therefore, by implication, close relatives) or in opposite directions (therefore, distant relatives). A single test supplies only two dimensions of a three dimensional arrangement.

It is impossible to interpret and to picture the serological data satisfactorily in two dimensions; therefore, a three-dimensional model (Figs. 22, 23) was constructed to summarize the serological relationships of the birds involved. Each of the eleven kinds used consistently throughout the investigation is represented in the model. By use of the percentage values (Table 2), each bird was located in relation to the other birds. Where possible, averages of reciprocal tests (Table 3) were used in determining distances between the elements of the model. In this way seven of the birds were accurately located in relation to each other. Lacking reciprocal tests, the positions of the other birds were determined by the values of single tests (Table 4). Although these birds were placed with less certainty, at least four points of reference were used in locating each species. At least one serological test is represented by each connecting bar in the model. The lengths of the bars connecting any two elements were determined as follows: a percentage value (Table 3 and Table 4) representing the degree of serological correspondence between two birds was subtracted from 100 per cent; the remainder was multiplied by a factor of five to increase the size of the model and the product was expressed in millimeters; a bar of proper length connects the two elements involved.

From the model it is observed that, *Molothrus* and *Passer* excluded, the birds fall into two distinct groups: one includes *Piranga*, *Richmondena*, *Spiza*, *Junco*, and *Zonotrichia*; the other includes *Estrilda*, *Poephila*, *Carpodacus*, and *Spinus*.

TABLE 3.—RECIPROCAL VALUES USED TO DETERMINE DISTANCES BETWEEN ELEMENTS OF THE MODEL; EACH VALUE REPRESENTS THE AVERAGE OF SEROLOGICAL TESTS BETWEEN THE SPECIES INVOLVED [Pg 194]

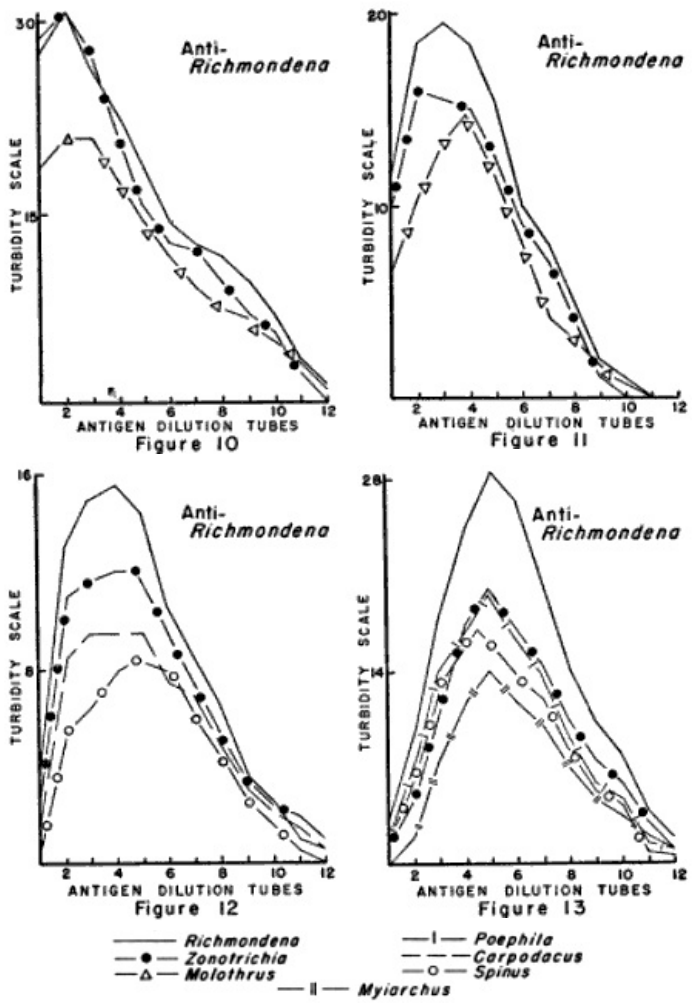
	Estrilda amandava	*Poephila guttata*	*Richmondena cardinalis*	*Spiza americana*	*Spinus tristis*	*Junco hyemalis*	*Zonotrichia querula*
	..	92	..	72	72	59	..

Estrilda amandava							
Poephila guttata	92	..	74	78	78	..	..
Richmondena cardinalis	..	74	..	85	63	77	79
Spiza americana	72	78	85	..	77	77	85
Spinus tristis	72	78	63	77	..	..	..
Junco hyemalis	..	..	77	77	..	..	..
Zonotrichia querula	..	..	79	85	..	..	..

TABLE 4.—SINGLE VALUES USED TO DETERMINE DISTANCES BETWEEN ELEMENTS OF THE MODEL; EACH VALUE REPRESENTS A SINGLE TEST BETWEEN THE SPECIES INVOLVED

	Estrilda amandava	*Poephila guttata*	*Piranga rubra*	*Richmondena cardinalis*	*Spinus tristis*	*Junco hyemalis*	*Zonotrichia querula*
Passer domesticus	..	74	73	..	72	..	..
Molothrus ater	..	54	..	65	..	69	75
Piranga rubra	..	77	..	91	73	74	..
Carpodacus purpureus	70	71	..	61	93	..	..

[Pg 195]

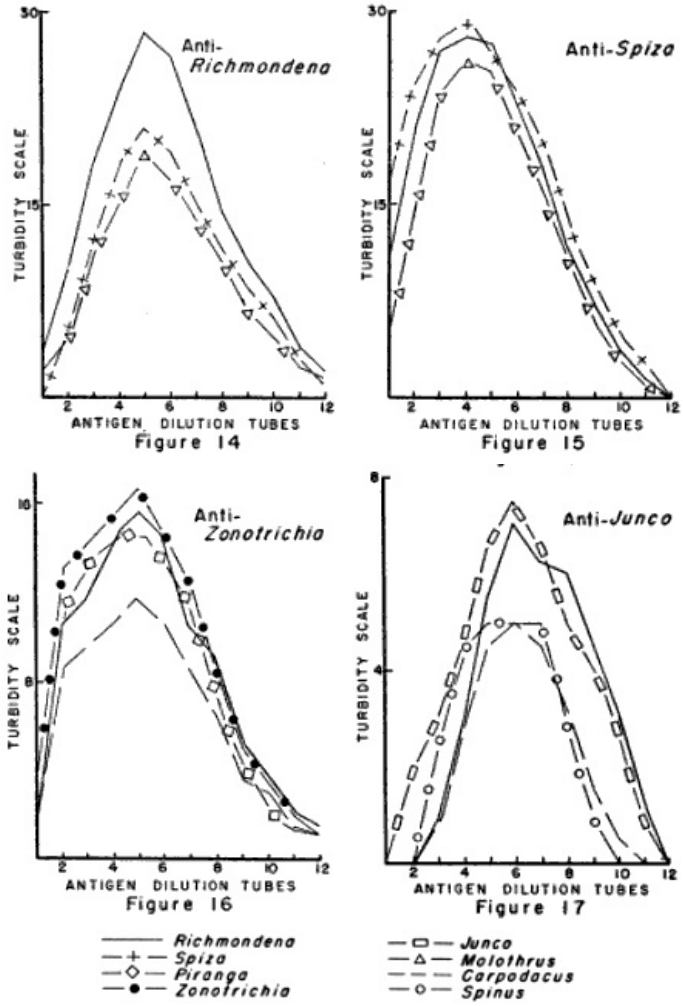


FIGS. 10-13. Graphs of precipitin reactions illustrating effects of formalin on antigenicity and reactivity of the extracts. For further information, see text, pp. 190-193.

FIG. 10. Reactions of unformolized antigens of *Richmondena*, *Zonotrichia*, and *Molothrus* with anti-*Richmondena* serum. FIG. 11. Reactions of formolized antigens of *Richmondena*, *Zonotrichia*,

and *Molothrus* with anti-*Richmondena* serum. Fig. 12. Reactions of anti-*Richmondena* serum prepared against native antigen with antigens of *Richmondena*, *Zonotrichia*, *Carpodacus*, and *Spinus*. Fig. 13. Reactions of anti-*Richmondena* serum prepared against formolized antigen with antigens of *Richmondena*, *Zonotrichia*, *Poephila*, *Spinus*, and *Myiarchus*.

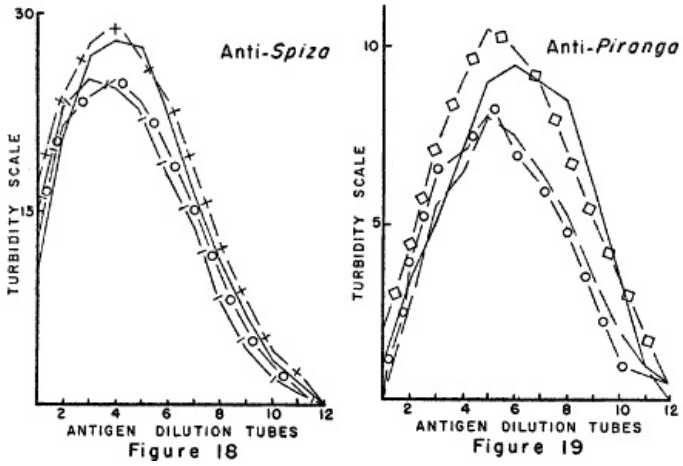
[Pg 196]

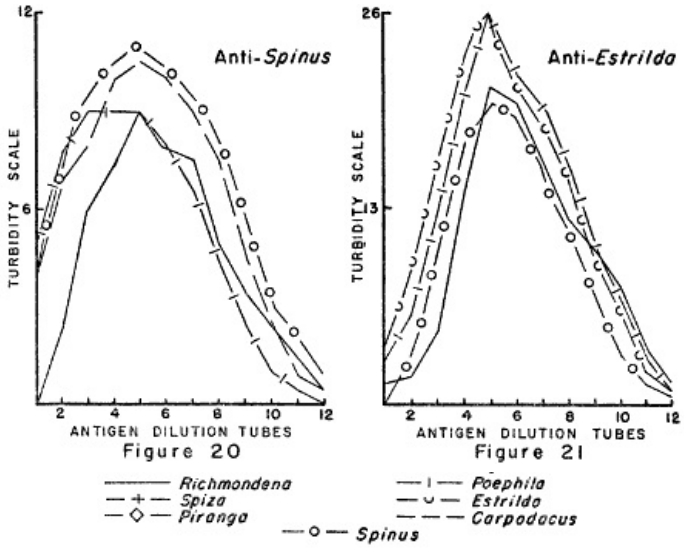


Figs. 14-17. Graphs of precipitin reactions illustrating serological relationships. For further explanation, see text, pp. 190-193.

Fig. 14. Serological relationships of *Richmondena*, *Spiza*, and *Molothrus*. Fig. 15. Serological relationships of *Richmondena*, *Spiza*, and *Molothrus*. Fig. 16. Serological relationships of *Carpodacus* with the richmondenine-emberizine-thraupid assemblage. Fig. 17. Serological relationships of *Carpodacus* and *Spinus* with *Richmondena* and *Junco*.

[Pg 197]





FIGS. 18-21. Graphs of precipitin reactions illustrating serological relationships. For further explanation, see text, pp. 190-193.

FIG. 18. Serological relationships of *Spinus* and *Poephila* with the richmondenines. FIG. 19. Serological relationships of *Carpodacus* and *Spinus* with *Richmondena* and *Piranga*. FIG. 20. Serological relationships of *Poephila* and Richmondena with the carduelines. FIG. 21. Serological relationships of *Richmondena* and *Spinus* with the estrildines.

[Pg 198]

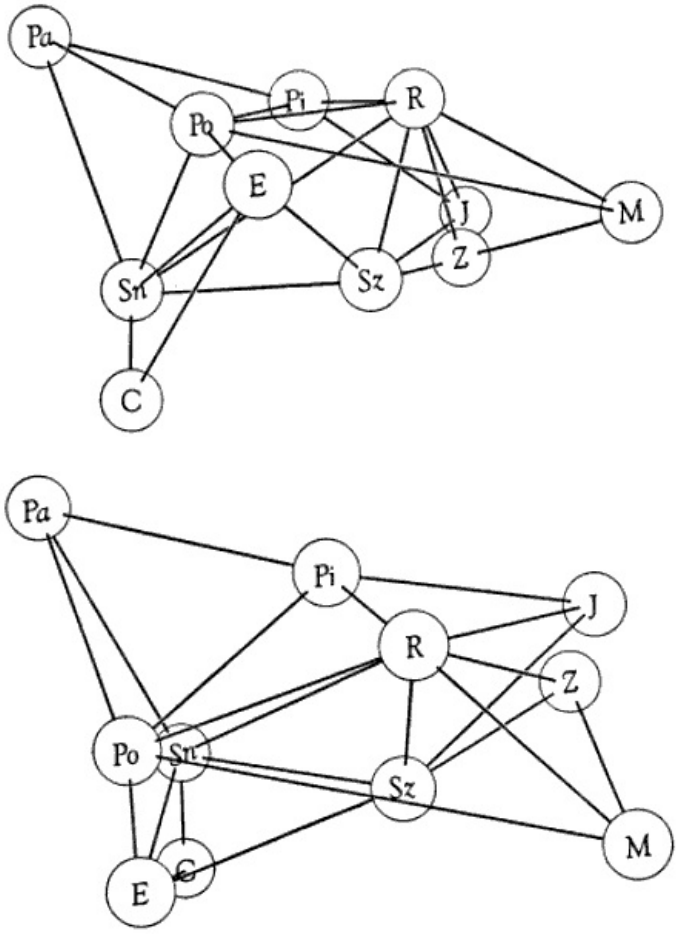


FIG. 22. Two views of a model illustrating serological relationships among fringillid and related birds. For further explanation, see text, pp. 193-194.

Genera					
C	. . . .	*Carpodacus*	Pi	. . . .	*Piranga*
E	. . . .	*Estrilda*	Po	. . . .	*Poephila*
J	. . . .	*Junco*	R	. . . .	*Richmondena*
M	. . . .	*Molothrus*	Sn	. . . .	*Spinus*
Pa	. . . .	*Passer*	Sz	. . . .	*Spiza*
			Z	. . . .	*Zonotrichia*

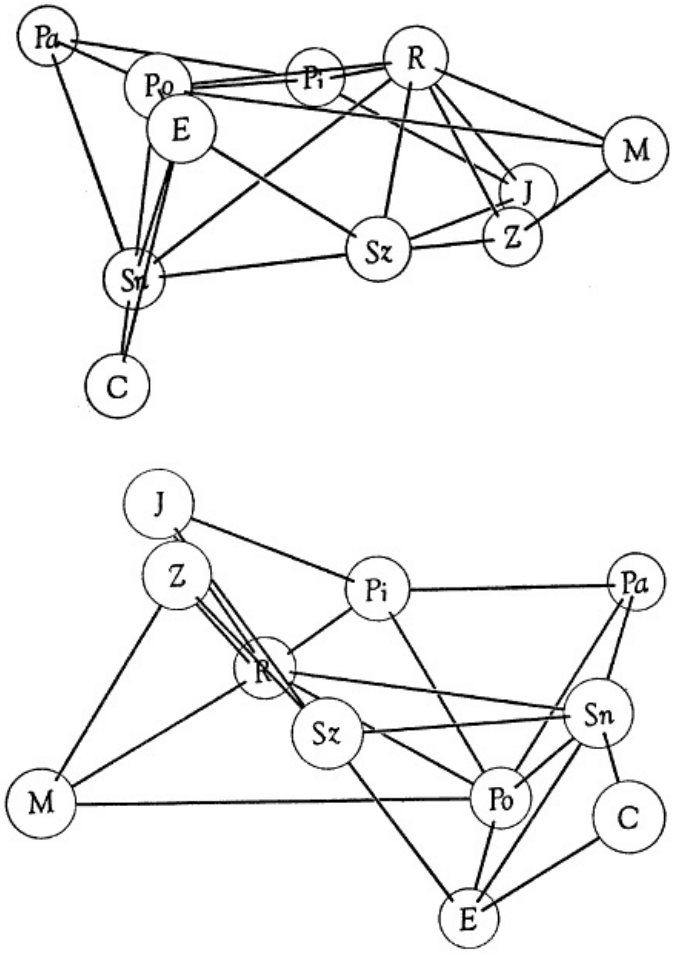


FIG. 23. Two additional views of the model shown in fig. 22 illustrating serological relationships among fringillid and related birds. For further explanation, see text, pp. 193-194.

	Genera				
C	. . . .	*Carpodacus*	Pi	. . . .	*Piranga*
E	. . . .	*Estrilda*	Po	. . . .	*Poephila*
J	. . . .	*Junco*	R	. . . .	*Richmondena*
M	. . . .	*Molothrus*	Sn	. . . .	*Spinus*
Pa	. . . .	*Passer*	Sz	. . . .	*Spiza*
			Z	. . . .	*Zonotrichia*

Within the richmondenine-emberizine-thraupid assemblage, *Junco* and *Zonotrichia* constitute a sub-group apart from the others. *Piranga* and *Richmondena* show close serological correspondence. The present taxonomic position of *Spiza* in the Richmondeninae, which has been questioned by Beecher (1951a:431; 1953:309), is corroborated at least insofar as the serological evidence is concerned. Certainly, serological correspondence of *Spiza* with the richmondenine-emberizine-thraupid assemblage is greater than with any other group of birds tested.

It is obvious that the serological affinities of the carduelines do not lie with the richmondenines, emberizines, or thraupids. The carduelines show greater serological correspondence with the estrildines than they do with any of the other groups tested. Further serological investigation involving other species, however, is necessary before the nearest relatives of the carduelines can be determined with certainty.

The two estrildines tested (*Estrilda* and *Poephila*) show close serological relationship. Their nearest relatives, serologically, seem to be the carduelines. The classification (Wetmore, 1951) that places *Passer* in the same family with the estrildines is not upheld by the serological data available. *Passer* is not, serologically, closely related to any of the birds tested. It is of interest that Beecher (1953:303-305), on the basis of jaw musculature, places *Passer* and the estrildines in separate families (Ploceidae and Estrildidae, respectively).

Molothrus shows greater serological correspondence to the richmondenine-emberizine-thraupid assemblage than to any of the other birds tested. It is definitely set apart from this group, however, and its position, serologically, is compatible with that based on evidence from

other sources.

There seems to be but little argument among ornithologists that icterids, fringillids, and ploceids constitute families which are distinct from one another. If, then, the serological differences between *Molothrus* (Icteridae) and *Richmondena* (Fringillidae), between *Molothrus* and *Zonotrichia* (Fringillidae), and between *Richmondena* and *Poephila* (Ploceidae) are indicative of family differences, there are four families represented by the birds involved. *Molothrus* represents one family; *Piranga*, *Richmondena*, *Spiza*, *Junco*, and *Zonotrichia*, a second; *Estrilda*, *Poephila*, *Carpodacus*, and *Spinus*, a third; and *Passer*, a fourth.

[↑ TOC]

Conclusions

The heterogeneity of the Family Fringillidae has been emphasized by many authors. The relationships of the species now included in this Family have been the subject of much discussion and constitute an important problem in avian systematics.

Sushkin's studies (1924, 1925) of features of the horny and bony palates have served as a basis for the present division of the Family into subfamilies. Recently, Beecher (1951a, 1951b, 1953) and Tordoff (1954) have used these features and others which they thought to be of value in an attempt to clarify the relationships of the species involved.

Beecher's work (1951a, 1951b, 1953) on jaw-musculature is a valuable contribution to our knowledge of the anatomy of passerine birds. His myological studies were so thorough and his presentation so detailed that students who disagree with his interpretations can draw their own conclusions. Beecher (1951b:276) points out that there are two basic types of skeletal muscle—those with parallel fibers and those with pinnately arranged fibers. The muscles with pinnate fibers seem to be more efficient, each muscle having a greater functional cross section for its bulk than does one with parallel fibers. He assumes that muscles with parallel fibers are more primitive, phylogenetically, than are those with fibers arranged pinnately. Since his study of the jaw muscles of the Icteridae (1951a) revealed that patterns of jaw-musculature within this Family remain constant regardless of the methods used in procuring food, he assumes that such patterns may be used as indicators of relationship throughout the entire oscinine group. These two assumptions, then, serve as the basis for his hypothesis concerning relationship and phylogeny within this assemblage. Beecher (1951b:278-280; 1953:310-312) maintains that within the Family Thraupidae there are two main lines which lead with almost no disjunction to the Carduelinae and Richmondeninae. The thraupid-richmondenine line involves a shift in the nature of the *m. adductor mandibulae externus superficialis*, which becomes more pinnate in the richmondenines. This results in greater crushing power. The thraupid-cardueline line involves a shift in emphasis from the the *m. adductor mandibulae externus medialis* to the *m. pseudotemporalis superficialis* and the forward advance of the insertion of the latter. This, also, promotes greater crushing ability. He states that features of the horny palate and of the plumage provide further evidence of close relationship of these groups. He includes, therefore, the Thraupinae, the Carduelinae, and the Pyrrhuloxiinae (=Richmondeninae) in the Family Thraupidae. Beecher (1953:307) indicates that the patterns of jaw-musculature of the Parulinae (wood warblers) and Emberizinae (buntings) are similar and suggests that the buntings had their origin from the wood warblers. He includes these subfamilies, therefore, in the Family Parulidae.

Beecher's reasoning may be criticized on several points. It may be, as he suggests, that muscles with parallel fibers evolved earlier, phylogenetically, than did muscles with pinnate fibers, but he does not give adequate consideration, it seems to me, to the possibility that parallel fibers may also have evolved secondarily from pinnate fibers. Since Beecher (1951a) found that patterns of jaw-musculature within the Family Icteridae were conservative, he is reluctant to admit the possibility of convergence among any of the other families. Differences in patterns of jaw-musculature are, however, functional adaptations and like the bill, which is also associated with food-getting may be subject to rapid evolutionary change. Finally, in attempting to classify the oscines, he has relied almost entirely on a single character—the pattern of jaw-musculature.

Tordoff's attempts (1954) to clarify the relationships of the fringillids and related species are based chiefly on features of the bony palate. He assumes that since palato-maxillaries seem to be absent in the majority of passerine birds, their occurrence in certain nine-primaried oscine groups indicates relationship among these groups. He points out that these bones, when present, are important areas of origin of the *m. pterygoideus* which functions in depression of the upper jaw and in elevation of the lower jaw. He assumes, therefore, that palato-maxillaries were evolved to provide for a more effective action of the *m. pterygoideus*. The need for such action could be associated with a seed-eating habit. All richmondenines and emberizines possess palato-maxillary bones either free or fused to the prepalatine bar, but there is no trace of these bones in the carduelines. Carduelines, furthermore, possess prepalatine bars that are characteristically flared anteriorly. This condition does not exist in the richmondenines or in the emberizines.

Tordoff points out, also, that the irregular, erratic migrations of the New World Carduelinae

are unlike the more regular migrations of the richmondenines and emberizines. The carduelines, furthermore, are more arboreal in their habits than are these other groups and exhibit a decided lack of nest sanitation during the later stages of nesting, a situation which contrasts with that found in the Richmondeninae and Emberizinae. He suggests, therefore, that the carduelines are [Pg 203] not so closely related to the richmondenines and the emberizines as previously has been thought.

Since there are only two cardueline genera, *Loximitris* and *Hesperiphona*, endemic to the New World and at least 10 genera with many species endemic to the Old World, Tordoff (1954:15) suggests an Old World origin for the carduelines. He strengthens his argument for this hypothesis by pointing out that in features of the bony palate and in habits the carduelines resemble the estrildines of the Family Ploceidae.

Tordoff (1954:29-30) states that the tanagers not only merge with the richmondenines but also grade imperceptibly into the emberizines. He includes, therefore, the Richmondeninae, Emberizinae, and Thraupinae in the Family Fringillidae. He suggests that the carduelines are ploceids, closely related to the Subfamily Estrildinae, on the basis of structure of the bony palate, geographic distribution, social behavior, and habits such as nest-fouling and nest-building.

Tordoff, like Beecher, has based his interpretations chiefly on one feature—structure of the bony palate. Since this feature also is associated with food-getting, the possibilities of convergence of distantly related species with similar habits and divergence of closely related species with different habits may not be excluded.

The hazard of unrecognized adaptive convergence cannot, of course, be excluded from most fields of taxonomic research, but some features of morphology and biochemistry are notably more conservative than others and undergo slower evolutionary change. Such features are often of utmost importance in distinguishing the higher taxonomic categories.

Most ornithologists are aware that, within the Order Passeriformes, patterns of musculature in the leg have evolved at a slow rate and exhibit little variation within the Order. Differences which do occur, therefore, probably are significant, especially those that are consistent between groups of species. As I have pointed out earlier (p. 184), there are no significant differences in leg-musculature between the Richmondeninae, Emberizinae, and Thraupidae. Indeed, it is difficult to define these groups on the basis of leg-musculature. If these groups are of common origin, the lack of distinct boundaries between them is not surprising. A muscular band which extends from the *pars interna* of the *m. gastrocnemius* around the front of the knee is present in every emberizine species that I studied and in the Genus *Piranga*. With the exception of *Spiza* none of the richmondenines possesses this band.

The significant differences in leg-musculature which have been discussed above (pp. 183-184) [Pg 204] distinguish the carduelines from the New World finches and tanagers. Even the cardueline *Leucosticte* and the emberizine *Calcarius*, which resemble one another in general adaptations and in several myological features of the leg (p. 183), agree in significant features of the musculature with the respective groups to which they belong. The carduelines agree in the major features of leg-musculature with the ploceids which I studied.

The use of serological techniques in taxonomic work has two main advantages. The biochemical systems involved in such investigations seem to be relatively slow to change in response to external environmental influences, and the quantitative nature of the results obtained makes possible objective measurement of resemblances among species.

I have pointed out (p. 200) that the carduelines are excluded, serologically, from the distinct assemblage formed by the richmondenines, emberizines, and tanagers. Actually, the carduelines show less serological resemblance to this assemblage than do the estrildines, and most ornithologists agree that the Estrildinae are not at all closely related to the Richmondeninae, Emberizinae, and Thraupidae. *Molothrus*, representing a family (Icteridae) recognized as distinct from the Family Fringillidae, also more closely resembles the fringillid assemblage, serologically, than do the carduelines. Although the Carduelinae constitute a distinct group serologically, they show greater serological resemblance to the estrildines of the Family Ploceidae than to any of the other species tested. At least the carduelines and the estrildines form a group as compact as the subfamilies of the Fringillidae. Thus, the serological data correlate well with those obtained from the study of the leg-musculature.

Present systems of classification include the subfamilies Passerinae and Estrildinae in the Family Ploceidae. *Passer*, however, is less closely related to the estrildines serologically than are the carduelines, and is less closely related to the estrildines than *Molothrus*, an icterid, is to the fringillids. This raises a question as to the homogeneity of the Family Ploceidae as presently recognized by most ornithologists. If the Passerinae and the Estrildinae are placed in a single family, the serological divergence among members of this group is certainly greater than it is in the Family Fringillidae. Additionally, Beecher (1953:303-304) found that the estrildines possess a pattern of jaw-musculature different from those in other ploceids.

The combined evidence from jaw-musculature and serology has caused me to conclude that [Pg 205] the estrildines should be excluded from the Family Ploceidae (see below).

In an attempt to clarify the relationships of the Fringillidae and allied groups, I here review

briefly the evidence which has been presented. From his studies of jaw-musculature (1951a, 1951b, 1953) Beecher concludes that the Pyrrhuloxinae (=Richmondeninae), the Carduelinae, and the Thraupinae are closely related. He places these groups in the Family Thraupidae. He excludes the Emberizinae from this group and places them with the wood warblers in the Family Parulidae. He suggests that the estrildines constitute a family (Estrildidae) separate from the Family Ploceidae.

From his studies of certain features of the bony palate Tordoff (1954:25-26, 32) concludes that the richmondenines, the emberizines, and the tanagers have a common origin and places these groups in the Family Fringillidae. He excludes the carduelines from this assemblage, suggests that they are closely related to the estrildines, and includes them as the Subfamily Carduelinae in the Family Ploceidae.

In this paper I have presented data obtained from the study of certain features of morphology and biochemistry which I think are less subject to the influence of environmental factors than those features studied by recent workers. It is significant that the data obtained by use of serological techniques and those obtained from the study of leg-musculature point to the same conclusions. On the basis of these data I have drawn several conclusions concerning the relationships of the groups which I studied.

The richmondenines, emberizines, and tanagers are closely related and should be included in a single family, Fringillidae. The Carduelinae and the Estrildinae are closely related subfamilies. Although most recent classifications place the Estrildinae and Passerinae in the Family Ploceidae, the serological evidence indicates that these groups are not closely related. Beecher (1953:303-304) drew the same conclusion from his study of jaw-musculature (see above). I suggest, therefore, that the Carduelinae and the Estrildinae be placed in a family separate from the Ploceidae and that the name Carduelidae (rather than Estrildidae) be used for this group. At present, neither is an accepted family name. Because *Carduelis* Brisson 1760 is an older name than *Estrilda* Swainson 1827 and because *Carduelis* seems to be a centrally located genus in the family, I have chosen the former (although the International Rules of Zoological Nomenclature do not specify that priority must apply in forming family names). [Pg 206]

I have been unable to study any of the species included in the subfamilies Fringillinae (not Fringillinae of Tordoff, see 1954:23-24, and below) and Geospizinae of recent classifications; thus these groups have not been discussed above. Beecher (1953:307-308) includes *Fringilla* in the Subfamily Carduelinae; he includes the geospizines in a separate family, Geospizidae, and states that they are derived from the emberizines. Tordoff (1954:23-24) found that in features of the bony palate *Fringilla* and the geospizines resemble the emberizines and, on this basis, includes them in the Subfamily Fringillinae.

The Dickcissel, *Spiza americana*, possesses certain features which merit special discussion. Beecher (1951a:431; 1953:309), on the basis of jaw-musculature, considers it an icterid. To be sure *Spiza* is in many ways an aberrant member of the group to which it is now assigned (Subfamily Richmondeninae). *Spiza*, serologically, is closely related to all species of the richmondenine-emberizine-thraupid assemblage. Within this assemblage its nearest relatives are the richmondenines. *Spiza* differs from the other richmondenines studied and resembles the emberizines and tanagers in the possession of the muscular band which extends from the *pars interna* of the *m. gastrocnemius* around the front of the knee. This band, in *Spiza*, is smaller, however, than in any of the other species. No icterid dissected possesses such a structure. Tordoff (1954:29) states that *Spiza* is typically richmondenine in palatal structure and makes the suggestion, with which I agree, that *Spiza* is a richmondenine and may be closely related to the ancestral stock which gave rise to the fringillid assemblage. The serological position of *Spiza*, approximately equidistant from the other fringillids (Figs. 22, 23), and the presence of the small muscular band around the front of the knee constitute evidence supporting the central position of *Spiza*.

After consideration of evidence from the studies of external morphology, ethology, myology, osteology, and serology, I propose here an arrangement of the groups which I have studied and submit for comparison the arrangements (of these groups) proposed by Beecher and Tordoff. The names of subfamilies that I have been unable to study are included in my classification and are placed in brackets.

[Pg 207]

Here proposed	Proposed by Tordoff (1954) on the basis of the bony palate:	Proposed by Beecher (1953) on the basis of jaw-musculature:
Family Ploceidae [Subf. Bubalornithinae] Subfamily Passerinae: distinguished from the Estrildinae by patterns of jaw-musculature (Beecher,	Family Ploceidae Subf. Bubalornithinae Subfamily Passerinae	Family Ploceidae Subfamily Passerinae

1953:303-304) and on the basis of comparative serology of saline-soluble proteins. [Subfamily Ploceinae] [Subfamily Viduinae]	Subfamily Ploceinae Subfamily Viduinae	Subfamily Ploceinae Subfamily Viduinae
Family Carduelidae Subfamily Estrildinae: similar to the Carduelinae in features of the bony palate and habits (Tordoff, 1954: 18-22) and in patterns of leg-musculature and comparative serology of saline-soluble proteins. Subfamily Carduelinae: distinguished from the Fringillidae by features of the palate, geographic distribution, migration patterns, and habits (Tordoff, 1954: 14-18) and by patterns of leg-musculature and comparative serology of saline-soluble proteins.	Subfamily Estrildinae Subfamily Carduelinae	Family Estrildidae [In Thraupidae below]
Family Fringillidae: all members of this family show similarities in features of the bony palate (Tordoff, 1954: 22-23), patterns of leg-musculature, and in comparative serology of saline-soluble proteins. Subf. Richmondeninae Subfamily Thraupinae Subfamily Emberizinae [Subfamily Fringillinae] [Subfamily Geospizinae]	Family Fringillidae Subf. Richmondeninae Subfamily Thraupinae Subfamily Fringillinae (including Emberizinae and Geospizinae)	Family Parulidae Subfamily Parulinae Subfamily Emberizinae Family Thraupidae Subfamily Pyrrhuloxiinae Subfamily Thraupinae [In Parulidae above] Subfamily Carduelinae

[↑ TOC]

Summary

It has long been recognized that the Family Fringillidae includes some dissimilar groups. Specifically, the relationships of the subfamilies Richmondeninae, Emberizinae, and Carduelinae of the Family Fringillidae are poorly understood. Data from two recent studies, one on patterns of jaw-musculature and the other on features of the bony palate, emphasize the dissimilarity of these subfamilies but have given rise to conflicting concepts of the relationships of subfamilies within the Family.

This paper reports the results of studies involving morphological and biochemical features that I consider less sensitive to external environmental factors than are features which have been studied previously. Patterns of leg-musculature were chosen for study because earlier work showed that muscle patterns in the legs of passerine birds are highly stable and vary but little. Variations, therefore, which are consistent in separating groups of species should be significant. Serological techniques were used because the biochemical systems involved seem to be relatively slow to change in response to environmental influences and because the data obtained may be used in a highly objective manner to measure resemblance among species.

Individual differences in the patterns of leg-musculature were found to be slight and involved mainly the sizes and shapes of muscles. For this reason variations involving origin, insertion, or relative position of a muscle, were judged significant. In leg-musculature the Richmondeninae, the Emberizinae, and the Thraupidae resemble one another closely. Several differences in muscle pattern were found, however, which distinguish these groups from the Carduelinae. The leg-musculature of the carduelines closely resembles that of the Ploceidae.

Serological techniques involved the extraction of saline-soluble proteins from the tissues of the species to be studied. These extracts were carefully processed and were used as antigens. Formolization of the antigens was necessary as a means of preventing denaturation of the proteins by enzymatic activity. Antisera were produced in rabbits. The method of testing involved

turbidimetric analysis of the precipitin reaction. Utilizing the values for the precipitin tests a model was constructed which showed the relationships of the eleven species used in these tests. From a study of the model and the data used in its construction, it was determined that the Richmondeninae, Emberizinae, and Thraupidae constitute an assemblage distinct from the other species studied. The Carduelinae are excluded from the assemblage and serologically are most closely related to the Estrildinae. The estrildines, serologically, do not closely resemble *Passer*, Subfamily Passerinae, although recent classifications place these two subfamilies in the Family Ploceidae. [Pg 209]

Upon consideration of all evidence now available—from external morphology, ethology, myology, osteology, and serology—several hypotheses regarding the relationships of the groups studied are set forth. The richmondenines, emberizines, and tanagers are closely related subfamilies and are here included in the Family Fringillidae. The Estrildinae and Carduelinae are closely related subfamilies, but neither group is closely related to the Passerinae. The estrildines and carduelines, therefore, are placed in a separate family, the Carduelidae. In some ways, *Spiza* is an aberrant member of the Subfamily Richmondeninae but should be retained in that subfamily. It is suggested that *Spiza* is a primitive richmondenine closely related to the ancestral fringillid stock.

[↑ TOC]

Literature Cited

[Pg 210]

American Ornithologists' Union

1931. Check-list of North American birds. Fourth edition. Lancaster, Pa., xix + 526 pp.

Beecher, W. J.

1951a. Adaptations for food-getting in the American blackbirds. Auk, 68:411-440, 11 figs.
1951b. Convergence in the Coerebidae. Wilson Bull., 63:274-287, 5 figs.
1953. A phylogeny of the oscines. Auk, 70:270-333, 18 figs.

Berger, A. J.

1952. The comparative functional morphology of the pelvic appendage in three genera of Cuculidae. Amer. Mid. Nat., 47:513-605, 29 pls.

Boyden, A.

1942. Systematic serology: a critical appreciation. Physiol. Zool., 15:109-145, 12 figs.

Chapin, J. P.

1917. The classification of the weaver-birds. Bull. Amer. Mus. Nat. Hist., 37:243-280, 10 pls., 9 figs.

Cumley, R. W.

, and

Irwin, M. R.

1941. Pictorial representation of the antigenic differences between two dove species. Jour. Hered., 32:178-182, frontispiece, 2 figs.
1941. Interaction of antigens in dove hybrids. Ibid., 429-434, 3 figs.
1944. The correlation between antigenic composition and geographic range in the Old and New World of some species of *Columba*. Amer. Nat., 78:238-256, 1 fig.

DeFalco, R. J.

1942. A serological study of some avian relationships. Biol. Bull., 83:205-218.

Fisher, H. I.

1946. Adaptations and comparative anatomy of the locomotor apparatus of New World vultures. Amer. Mid. Nat., 35:545-727, 13 pls., 28 figs.

Gadow, H.

, and

Selenka, E.

1891. Vögel, vol. I, Anatomischer Theil. In Bronn's Klassen und Ordnungen des Thier-Reichs, Sechster Band, Vierte Abtheilung. Leipzig, 1008 pp., 59 pls.

Garrod, A. H.

1873. On certain muscles in the thigh of birds and their value in classification. Proc. Zool. Soc. London, Part I:626-644, 6 figs.
1874. On certain muscles in the thigh of birds and their value in classification. Ibid., Part II:111-123.

Greenberg, D. M.

1929. The colorimetric determination of serum proteins. J. Biol. Chem., 82:545-550.

Hellmayr, C. E.

1935. Catalogue of birds of the Americas. Field Mus. Nat. Hist., Zool. ser. 13, pt. 8, vi + 541 pp.
1936. Catalogue of birds of the Americas. Ibid., 13, pt. 9, v + 458 pp.
1937. Catalogue of birds of the Americas. Ibid., 13, pt. 10, v + 228 pp.
1938. Catalogue of birds of the Americas. Ibid., 13, pt. 11, vi + 662 pp.

Howard, H.

1929. The avifauna of the Emeryville shellmound. Univ. California Publ. Zool., 32:301-394, 3 pls., 54 figs.

Hudson, G. E.

1937. Studies on the muscles of the pelvic appendage in birds. Amer. Mid. Nat., 18:1-108, 26 pls.

Irwin, M. R.

1953. Evolutionary patterns of antigenic substances of the blood corpuscles in Columbidae. Evol., 7:31-50.

Irwin, M. R.

, and

Cole, L. J.

1936. Immunogenetic studies of species and of species hybrids in doves, and the separation of species-specific substances in the backcross. Jour. Exp. Zool., 73:85-108, 1 fig.

Leone, C. A.

1949. Comparative serology of some brachyuran crustacea and studies in hemocyanin correspondence. Biol. Bull., 97:273-286, 3 figs.
1953. Some effects of formalin on the serological activity of crustacean and mammalian sera. Jour. Immun., 70:386-392, 2 figs.

Libby, R. L.

1938. The photronreflectometer—an instrument for the measurement of turbid systems. Jour. Immun., 34:71-73, 1 fig.

Martin, E. P.

, and

Leone, C. A.

1952. Serological relationships among domestic fowl as shown by comparisons of protein preparations from corresponding organ systems. Trans. Kansas Acad. Sci., 55:439-444, 1 fig.

McGibbon, W. H.

1945. Further division of contrasting antigens in species hybrids in ducks. Genetics, 30:252-265.

Sasaki, K.

1928. Serological examination of the blood-relationship between wild and domestic ducks. Jour. Dept. Agri., Kyushu Imp. Univ., 2:117-132.

Simpson, G. G.

1944. Tempo and mode in evolution. Columbia Univ. Press, New York, xviii + 237 pp., 36 figs.

SUSHKIN, P. P.

1924. [On the Fringillidae and allied groups.] Bull. British Ornith. Club, 45:36-39.
1925. The evening grosbeak (Hesperiphona), the only American genus of a Palaearctic group. Auk, 42:256-261, 2 figs.

TORDOFF, H. B.

1954. A systematic study of the avian family Fringillidae, based on the structure of the skull. Univ. Michigan Mus. Zool. Misc. Publ. No. 81:1-42, 77 figs.

WETMORE, A.

1951. A revised classification for the birds of the world. Smithsonian Misc. Coll., 117(4):1-22.

Transmitted June 8, 1954.

25-4632

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Institutional libraries interested in publications exchange may obtain this series by addressing the Exchange Librarian, University of Kansas Library, Lawrence, Kansas. Copies for individuals, persons working in a particular field of study, may be obtained by addressing instead the Museum of Natural History, University of Kansas, Lawrence, Kansas. There is no provision for sale of this series by the University Library, which meets institutional requests, or by the Museum of Natural History, which meets the requests of individuals. Nevertheless, when individuals request copies from the Museum, 25 cents should be included, for each separate number that is 100 pages or more in length, for the purpose of defraying the costs of wrapping and mailing.

* An asterisk designates those numbers of which the Museum's supply (not the Library's supply) is exhausted. Numbers published to date, in this series, are as follows:

Vol. 1.
1. The pocket gophers (Genus Thomomys) of Utah. By Stephen D. Durrant. Pp. 1-82, 1 figure in text; August 15, 1946.
2. The systematic status of Eumeces pluvialis Cope, and noteworthy records of other amphibians and reptiles from Kansas and Oklahoma. By Hobart M. Smith. Pp. 85-89. August 15, 1946.
3. The tadpoles of Bufo cognatus Say. By Hobart M. Smith. Pp. 93-96, 1 figure in text. August 15, 1946.
4. Hybridization between two species of garter snakes. By Hobart M. Smith. Pp. 97-100. August 15, 1946.
5. Selected records of reptiles and amphibians from Kansas. By John Breukelman and Hobart M. Smith. Pp. 101-112. August 15, 1946.
6. Kyphosis and other variations in soft-shelled turtles. By Hobart M. Smith. Pp. 117-124, 3 figures in text. July 7, 1947.

canicaudus Miller. By E. Raymond Hall and Keith R. Kelson. Pp. 73-79. October 1, 1951.

8. A new pocket gopher (Genus Thomomys) from eastern Colorado. By E. Raymond Hall. Pp. 81-85. October 1, 1951.
9. Mammals taken along the Alaskan Highway. By Rollin H. Baker. Pp. 87-117, 1 figure in text. November 28, 1951.
*10. A synopsis of the North American Lagomorpha. By E. Raymond Hall. Pp. 119-202, 68 figures in text. December 15, 1951.
11. A new pocket mouse (Genus Perognathus) from Kansas. By E. Lendell Cockrum. Pp. 203-206. December 15, 1951.
12. Mammals from Tamaulipas, Mexico. By Rollin H. Baker. Pp. 207-218. December 15, 1951.
13. A new pocket gopher (Genus Thomomys) from Wyoming and Colorado. By E. Raymond Hall. Pp. 219-222. December 15, 1951.
14. A new name for the Mexican red bat. By E. Raymond Hall. Pp. 223-226. December 15, 1951.
15. Taxonomic notes on Mexican bats of the Genus Rhogeëssa. By E. Raymond Hall. Pp. 227-232. April 10, 1952.
16. Comments on the taxonomy and geographic distribution of some North American woodrats (Genus Neotoma). By Keith R. Kelson. Pp. 233-242. April 10, 1952.
17. The subspecies of the Mexican red-bellied squirrel, Sciurus aureogaster. By Keith R. Kelson. Pp. 243-250, 1 figure in text. April 10, 1952.
18. Geographic range of Peromyscus melanophrys, with description of new subspecies. By Rollin H. Baker. Pp. 251-258, 1 figure in text. May 10, 1952.
19. A new chipmunk (Genus Eutamias) from the Black Hills. By John A. White. Pp. 259-262. April 10, 1952.
20. A new piñon mouse (Peromyscus truei) from Durango, Mexico. By Robert B. Finley, Jr. Pp. 263-267. May 23, 1952.
21. An annotated checklist of Nebraskan bats. By Olin L. Webb and J. Knox Jones, Jr. Pp. 269-279. May 31, 1952.
22. Geographic variation in red-backed mice (Genus Clethrionomys) of the southern Rocky Mountain region. By E. Lendell Cockrum and Kenneth L. Fitch. Pp. 281-292, 1 figure in text. November 15, 1952.
23. Comments on the taxonomy and geographic distribution of North American microtines. By E. Raymond Hall and E. Lendell Cockrum. Pp. 293-312. November 17, 1952.
24. The subspecific status of two Central American sloths. By E. Raymond Hall and Keith R. Kelson. Pp. 313-337. November 21, 1952. [Pg iii]
25. Comments on the taxonomy and geographic distribution of some North American marsupials, insectivores, and carnivores. By E. Raymond Hall and Keith R. Kelson. Pp. 319-341. December 5, 1952.
26. Comments on the taxonomy and geographic distribution of some North American rodents. By E. Raymond Hall and Keith R. Kelson. Pp. 343-371. December 15, 1952.
27. A synopsis of the North American microtine rodents. By E. Raymond Hall and E. Lendell Cockrum. Pp. 373-498, 149 figures in text. January 15, 1953.
28. The pocket gophers (Genus Thomomys) of Coahuila, Mexico. By Rollin H. Baker. Pp. 499-514, 1 figure in text. June 1, 1953.
29. Geographic distribution of the pocket mouse, Perognathus fasciatus. By J. Knox Jones, Jr. Pp. 515-526, 7 figures in text. August 1, 1953.
30. A new subspecies of wood rat (Neotoma mexicana) from Colorado. By Robert B. Finley, Jr. Pp. 527-534, 2 figures in text. August 15, 1953.
31. Four new pocket gophers of the genus Cratogeomys from Jalisco, Mexico. By Robert J. Russell. Pp. 535-542. October 15, 1953.
32. Genera and subgenera of chipmunks. By John A. White. Pp. 543-561, 12 figures in text. December 1, 1953.
33. Taxonomy of the chipmunks, Eutamias quadrivittatus and Eutamias umbrinus. By John A. White. Pp. 563-582, 6 figures in text. December 1, 1953.
34. Geographic distribution and taxonomy of the chipmunks of Wyoming. By John A. White. Pp. 584-610, 3 figures in text. December 1, 1953.
35. The baculum of the chipmunks of western North America. By John A. White. Pp. 611-631, 19 figures in text. December 1, 1953.
36. Pleistocene Soricidae from San Josecito Cave, Nuevo Leon, Mexico. By James S. Findley. Pp. 633-639. December 1, 1953.
37. Seventeen species of bats recorded from Barro Colorado Island, Panama Canal Zone. By E. Raymond Hall and William B. Jackson. Pp. 641-646. December 1, 1953.

Index. Pp. 647-676.

*Vol. 6. (Complete) Mammals of Utah, *taxonomy and distribution*. By Stephen D. Durrant. Pp. 1-549, 91 figures in text, 30 tables. August 10, 1952.

Vol. 7. *1. Mammals of Kansas. By E. Lendell Cockrum. Pp. 1-303, 73 figures in text, 37 tables. August 25, 1952.
2. Ecology of the opossum on a natural area in northeastern Kansas. By Henry S. Fitch

and Lewis L. Sandidge. Pp. 305-338, 5 figures in text. August 24, 1953.

3. The silky pocket mice (Perognathus flavus) of Mexico. By Rollin H. Baker. Pp. 339-347, 1 figure in text. February 15, 1954.
4. North American jumping mice (Genus Zapus). By Philip H. Krutzsch. Pp. 349-472, 47 figures in text, 4 tables. April 21, 1954.
5. Mammals from Southeastern Alaska. By Rollin H. Baker and James S. Findley. Pp. 473-477. April 21, 1954.
6. Distribution of Some Nebraskan Mammals. By J. Knox Jones, Jr. Pp. 479-487. April 21, 1954.
7. Subspeciation in the montane meadow mouse, Microtus montanus, in Wyoming and Colorado. By Sydney Anderson. Pp. 489-506, 2 figures in text. July 23, 1954.
8. A new subspecies of bat (Myotis velifer) from southeastern California and Arizona. By Terry A. Vaughn. Pp. 507-512. July 23, 1954.
9. Mammals of the San Gabriel mountains of California. By Terry A. Vaughn. Pp. 513-582, 1 figure in text, 12 tables. November 15, 1954.

More numbers will appear in volume 7.

Vol. 8.
1. Life history and ecology of the five-lined skink, Eumeces fasciatus. By Henry S. Fitch. Pp. 1-156, 26 figs. in text. September 1, 1954.
2. Myology and serology of the Avian Family Fringillidae, a taxonomic study. By William B. Stallcup. Pp. 157-211, 23 figures in text, 4 tables. November 15, 1954.

More numbers will appear in volume 8.

work is unprotected by copyright law in the United States and you are located in the United States, we do not claim a right to prevent you from copying, distributing, performing, displaying or creating derivative works based on the work as long as all references to Project Gutenberg are removed. Of course, we hope that you will support the Project Gutenberg™ mission of promoting free access to electronic works by freely sharing Project Gutenberg™ works in compliance with the terms of this agreement for keeping the Project Gutenberg™ name associated with the work. You can easily comply with the terms of this agreement by keeping this work in the same format with its attached full Project Gutenberg™ License when you share it without charge with others.

1.D. The copyright laws of the place where you are located also govern what you can do with this work. Copyright laws in most countries are in a constant state of change. If you are outside the United States, check the laws of your country in addition to the terms of this agreement before downloading, copying, displaying, performing, distributing or creating derivative works based on this work or any other Project Gutenberg™ work. The Foundation makes no representations concerning the copyright status of any work in any country other than the United States.

1.E. Unless you have removed all references to Project Gutenberg:

1.E.1. The following sentence, with active links to, or other immediate access to, the full Project Gutenberg™ License must appear prominently whenever any copy of a Project Gutenberg™ work (any work on which the phrase “Project Gutenberg” appears, or with which the phrase “Project Gutenberg” is associated) is accessed, displayed, performed, viewed, copied or distributed:

> This eBook is for the use of anyone anywhere in the United States and most other parts of the world at no cost and with almost no restrictions whatsoever. You may copy it, give it away or re-use it under the terms of the Project Gutenberg License included with this eBook or online at www.gutenberg.org. If you are not located in the United States, you will have to check the laws of the country where you are located before using this eBook.

1.E.2. If an individual Project Gutenberg™ electronic work is derived from texts not protected by U.S. copyright law (does not contain a notice indicating that it is posted with permission of the copyright holder), the work can be copied and distributed to anyone in the United States without paying any fees or charges. If you are redistributing or providing access to a work with the phrase “Project Gutenberg” associated with or appearing on the work, you must comply either with the requirements of paragraphs 1.E.1 through 1.E.7 or obtain permission for the use of the work and the Project Gutenberg™ trademark as set forth in paragraphs 1.E.8 or 1.E.9.

1.E.3. If an individual Project Gutenberg™ electronic work is posted with the permission of the copyright holder, your use and distribution must comply with both paragraphs 1.E.1 through 1.E.7 and any additional terms imposed by the copyright holder. Additional terms will be linked to the Project Gutenberg™ License for all works posted with the permission of the copyright holder found at the beginning of this work.

1.E.4. Do not unlink or detach or remove the full Project Gutenberg™ License terms from this work, or any files containing a part of this work or any other work associated with Project Gutenberg™.

1.E.5. Do not copy, display, perform, distribute or redistribute this electronic work, or any part of this electronic work, without prominently displaying the sentence set forth in paragraph 1.E.1 with active links or immediate access to the full terms of the Project Gutenberg™ License.

1.E.6. You may convert to and distribute this work in any binary, compressed, marked up, nonproprietary or proprietary form, including any word processing or hypertext form. However, if you provide access to or distribute copies of a Project Gutenberg™ work in a format other than “Plain Vanilla ASCII” or other format used in the official version posted on the official Project Gutenberg™ website (www.gutenberg.org), you must, at no additional cost, fee or expense to the user, provide a copy, a means of exporting a copy, or a means of obtaining a copy upon request, of the work in its original “Plain Vanilla ASCII” or other form. Any alternate format must include the full Project Gutenberg™ License as specified in paragraph 1.E.1.

1.E.7. Do not charge a fee for access to, viewing, displaying, performing, copying or distributing any Project Gutenberg™ works unless you comply with paragraph 1.E.8 or 1.E.9.

1.E.8. You may charge a reasonable fee for copies of or providing access to or distributing Project Gutenberg™ electronic works provided that:

- You pay a royalty fee of 20% of the gross profits you derive from the use of Project Gutenberg™ works calculated using the method you already use to calculate your applicable taxes. The fee is owed to the owner of the Project Gutenberg™ trademark, but he has agreed to donate royalties under this paragraph to the Project Gutenberg Literary Archive Foundation. Royalty payments must be paid within 60 days following each date on which you prepare (or are legally required to prepare) your periodic tax returns. Royalty payments should be clearly marked as such and sent to the Project Gutenberg Literary Archive Foundation at the address specified in Section 4, “Information about donations to the Project Gutenberg Literary Archive Foundation.”
- You provide a full refund of any money paid by a user who notifies you in writing (or by e-mail)

within 30 days of receipt that s/he does not agree to the terms of the full Project Gutenberg™ License. You must require such a user to return or destroy all copies of the works possessed in a physical medium and discontinue all use of and all access to other copies of Project Gutenberg™ works.
- You provide, in accordance with paragraph 1.F.3, a full refund of any money paid for a work or a replacement copy, if a defect in the electronic work is discovered and reported to you within 90 days of receipt of the work.
- You comply with all other terms of this agreement for free distribution of Project Gutenberg™ works.

1.E.9. If you wish to charge a fee or distribute a Project Gutenberg™ electronic work or group of works on different terms than are set forth in this agreement, you must obtain permission in writing from the Project Gutenberg Literary Archive Foundation, the manager of the Project Gutenberg™ trademark. Contact the Foundation as set forth in Section 3 below.

1.F.

1.F.1. Project Gutenberg volunteers and employees expend considerable effort to identify, do copyright research on, transcribe and proofread works not protected by U.S. copyright law in creating the Project Gutenberg™ collection. Despite these efforts, Project Gutenberg™ electronic works, and the medium on which they may be stored, may contain “Defects,” such as, but not limited to, incomplete, inaccurate or corrupt data, transcription errors, a copyright or other intellectual property infringement, a defective or damaged disk or other medium, a computer virus, or computer codes that damage or cannot be read by your equipment.

1.F.2. LIMITED WARRANTY, DISCLAIMER OF DAMAGES - Except for the “Right of Replacement or Refund” described in paragraph 1.F.3, the Project Gutenberg Literary Archive Foundation, the owner of the Project Gutenberg™ trademark, and any other party distributing a Project Gutenberg™ electronic work under this agreement, disclaim all liability to you for damages, costs and expenses, including legal fees. YOU AGREE THAT YOU HAVE NO REMEDIES FOR NEGLIGENCE, STRICT LIABILITY, BREACH OF WARRANTY OR BREACH OF CONTRACT EXCEPT THOSE PROVIDED IN PARAGRAPH 1.F.3. YOU AGREE THAT THE FOUNDATION, THE TRADEMARK OWNER, AND ANY DISTRIBUTOR UNDER THIS AGREEMENT WILL NOT BE LIABLE TO YOU FOR ACTUAL, DIRECT, INDIRECT, CONSEQUENTIAL, PUNITIVE OR INCIDENTAL DAMAGES EVEN IF YOU GIVE NOTICE OF THE POSSIBILITY OF SUCH DAMAGE.

1.F.3. LIMITED RIGHT OF REPLACEMENT OR REFUND - If you discover a defect in this electronic work within 90 days of receiving it, you can receive a refund of the money (if any) you paid for it by sending a written explanation to the person you received the work from. If you received the work on a physical medium, you must return the medium with your written explanation. The person or entity that provided you with the defective work may elect to provide a replacement copy in lieu of a refund. If you received the work electronically, the person or entity providing it to you may choose to give you a second opportunity to receive the work electronically in lieu of a refund. If the second copy is also defective, you may demand a refund in writing without further opportunities to fix the problem.

1.F.4. Except for the limited right of replacement or refund set forth in paragraph 1.F.3, this work is provided to you ‘AS-IS’, WITH NO OTHER WARRANTIES OF ANY KIND, EXPRESS OR IMPLIED, INCLUDING BUT NOT LIMITED TO WARRANTIES OF MERCHANTABILITY OR FITNESS FOR ANY PURPOSE.

1.F.5. Some states do not allow disclaimers of certain implied warranties or the exclusion or limitation of certain types of damages. If any disclaimer or limitation set forth in this agreement violates the law of the state applicable to this agreement, the agreement shall be interpreted to make the maximum disclaimer or limitation permitted by the applicable state law. The invalidity or unenforceability of any provision of this agreement shall not void the remaining provisions.

1.F.6. INDEMNITY - You agree to indemnify and hold the Foundation, the trademark owner, any agent or employee of the Foundation, anyone providing copies of Project Gutenberg™ electronic works in accordance with this agreement, and any volunteers associated with the production, promotion and distribution of Project Gutenberg™ electronic works, harmless from all liability, costs and expenses, including legal fees, that arise directly or indirectly from any of the following which you do or cause to occur: (a) distribution of this or any Project Gutenberg™ work, (b) alteration, modification, or additions or deletions to any Project Gutenberg™ work, and (c) any Defect you cause.

Section 2. Information about the Mission of Project Gutenberg™

Project Gutenberg™ is synonymous with the free distribution of electronic works in formats readable by the widest variety of computers including obsolete, old, middle-aged and new computers. It exists because of the efforts of hundreds of volunteers and donations from people in all walks of life.

Volunteers and financial support to provide volunteers with the assistance they need are critical to reaching Project Gutenberg™’s goals and ensuring that the Project Gutenberg™ collection will

remain freely available for generations to come. In 2001, the Project Gutenberg Literary Archive Foundation was created to provide a secure and permanent future for Project Gutenberg™ and future generations. To learn more about the Project Gutenberg Literary Archive Foundation and how your efforts and donations can help, see Sections 3 and 4 and the Foundation information page at www.gutenberg.org.

Section 3. Information about the Project Gutenberg Literary Archive Foundation

The Project Gutenberg Literary Archive Foundation is a non-profit 501(c)(3) educational corporation organized under the laws of the state of Mississippi and granted tax exempt status by the Internal Revenue Service. The Foundation's EIN or federal tax identification number is 64-6221541. Contributions to the Project Gutenberg Literary Archive Foundation are tax deductible to the full extent permitted by U.S. federal laws and your state's laws.

The Foundation's business office is located at 809 North 1500 West, Salt Lake City, UT 84116, (801) 596-1887. Email contact links and up to date contact information can be found at the Foundation's website and official page at www.gutenberg.org/contact

Section 4. Information about Donations to the Project Gutenberg Literary Archive Foundation

Project Gutenberg™ depends upon and cannot survive without widespread public support and donations to carry out its mission of increasing the number of public domain and licensed works that can be freely distributed in machine-readable form accessible by the widest array of equipment including outdated equipment. Many small donations ($1 to $5,000) are particularly important to maintaining tax exempt status with the IRS.

The Foundation is committed to complying with the laws regulating charities and charitable donations in all 50 states of the United States. Compliance requirements are not uniform and it takes a considerable effort, much paperwork and many fees to meet and keep up with these requirements. We do not solicit donations in locations where we have not received written confirmation of compliance. To SEND DONATIONS or determine the status of compliance for any particular state visit www.gutenberg.org/donate.

While we cannot and do not solicit contributions from states where we have not met the solicitation requirements, we know of no prohibition against accepting unsolicited donations from donors in such states who approach us with offers to donate.

International donations are gratefully accepted, but we cannot make any statements concerning tax treatment of donations received from outside the United States. U.S. laws alone swamp our small staff.

Please check the Project Gutenberg web pages for current donation methods and addresses. Donations are accepted in a number of other ways including checks, online payments and credit card donations. To donate, please visit: www.gutenberg.org/donate

Section 5. General Information About Project Gutenberg™ electronic works

Professor Michael S. Hart was the originator of the Project Gutenberg™ concept of a library of electronic works that could be freely shared with anyone. For forty years, he produced and distributed Project Gutenberg™ eBooks with only a loose network of volunteer support.

Project Gutenberg™ eBooks are often created from several printed editions, all of which are confirmed as not protected by copyright in the U.S. unless a copyright notice is included. Thus, we do not necessarily keep eBooks in compliance with any particular paper edition.

Most people start at our website which has the main PG search facility: www.gutenberg.org.

This website includes information about Project Gutenberg™, including how to make donations to the Project Gutenberg Literary Archive Foundation, how to help produce our new eBooks, and how to subscribe to our email newsletter to hear about new eBooks.