

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 81

**A Systematic Study
of the Avian Family Fringillidae
Based on the Structure
of the Skull**

BY

HARRISON B. TORDOFF

ANN ARBOR
UNIVERSITY OF MICHIGAN PRESS

APRIL 26, 1954

PRICE LIST OF THE MISCELLANEOUS PUBLICATIONS
OF THE MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN

Address inquiries to the Director of the Museum of Zoology, Ann Arbor, Michigan

Bound in Paper

No. 1.	Directions for Collecting and Preserving Specimens of Dragonflies for Museum Purposes. By E. B. Williamson. (1916) Pp. 15, 3 figures	\$0.25
No. 2.	An Annotated List of the Odonata of Indiana. By E. B. Williamson. (1917) Pp. 12, 1 map	\$0.25
No. 3.	A Collecting Trip to Colombia, South America. By E. B. Williamson. (1918) Pp. 24 (Out of print)	
No. 4.	Contributions to the Botany of Michigan. By C. K. Dodge. (1918) Pp. 14	\$0.25
No. 5.	Contributions to the Botany of Michigan, II. By C. K. Dodge. (1918) Pp. 44, 1 map . .	\$0.45
No. 6.	A Synopsis of the Classification of the Fresh-water Mollusca of North America, North of Mexico, and a Catalogue of the More Recently Described Species, with Notes. By Bryant Walker. (1918) Pp. 213, 1 plate, 233 figures	\$3.00
No. 7.	The Anculosae of the Alabama River Drainage. By Calvin Goodrich. (1922) Pp. 57, 3 plates	\$0.75
No. 8.	The Amphibians and Reptiles of the Sierra Nevada de Santa Marta, Colombia. By Alexander G. Ruthven. (1922) Pp. 69, 13 plates, 2 figures, 1 map	\$1.00
No. 9.	Notes on American Species of Triacanthagyna and Gynacantha. By E. B. Williamson. (1923) Pp. 67, 7 plates	\$0.75
No. 10.	A Preliminary Survey of the Bird Life of North Dakota. By Norman A. Wood. (1923) Pp. 85, 6 plates, 1 map	\$1.00
No. 11.	Notes on the Genus <i>Erythemis</i> with a Description of a New Species (Odonata). By E. B. Williamson. The Phylogeny and the Distribution of the Genus <i>Erythemis</i> (Odonata). By Clarence H. Kennedy. (1923) Pp. 21, 1 plate	\$0.50
No. 12.	The Genus <i>Gyrotoma</i> . By Calvin Goodrich. (1924) Pp. 29, 2 plates	\$0.50
No. 13.	Studies of the Fishes of the Order Cyprinodontes. By Carl L. Hubbs. (1924) Pp. 23, 4 plates	\$0.75
No. 14.	The Genus <i>Perilestes</i> (Odonata). By E. B. Williamson and J. H. Williamson. (1924) Pp. 36, 1 plate	\$0.50
No. 15.	A Check-List of the Fishes of the Great Lakes and Tributary Waters, with Nomenclatorial Notes and Analytical Keys. By Carl L. Hubbs. (1926) Pp. 77, 4 plates	\$1.50
No. 16.	Studies of the Fishes of the Order Cyprinodontes. VI. By Carl L. Hubbs. (1926) Pp. 79, 4 plates	\$1.00
No. 17.	The Structure and Growth of the Scales of Fishes in Relation to the Interpretation of Their Life-History, with Special Reference to the Sunfish <i>Eupomotis gibbosus</i> . By Charles W. Creaser. (1926) Pp. 80, 1 plate, 12 figures	\$1.50
No. 18.	The Terrestrial Shell-bearing Mollusca of Alabama. By Bryant Walker. (1928) Pp. 180, 278 figures	\$1.50
No. 19.	The Life History of the Toucan <i>Ramphastos brevicarinatus</i> . By Josselyn Van Tyne. (1929) Pp. 43, 8 plates, 1 map	\$0.75
No. 20.	Materials for a Revision of the Catostomid Fishes of Eastern North America. By Carl L. Hubbs. (1930) Pp. 47, 1 plate	\$0.75
No. 21.	A Revision of the Libelluline Genus <i>Perithemis</i> (Odonata). By F. Ris. (1930) Pp. 50, 9 plates	\$0.75
No. 22.	The Genus <i>Oligoclada</i> (Odonata). By Donald Borrer. (1931) Pp. 42, 7 plates	\$0.50
No. 23.	A Revision of the Puer Group of the North American Genus <i>Melanoplus</i> , with Remarks on the Taxonomic Value of the Concealed Male Genitalia in the <i>Cyrtacanthacrinae</i> (Orthoptera, Acrididae). By Theodore H. Hubbell. (1932) Pp. 64, 3 plates, 1 figure, 1 map	\$0.75
No. 24.	A Comparative Life History Study of the Mice of the Genus <i>Peromyscus</i> . By Arthur Svihla. (1932) Pp. 39	\$0.50
No. 25.	The Moose of Isle Royale. By Adolph Murie. (1934) Pp. 44, 7 plates	\$0.70
No. 26.	Mammals from Guatemala and British Honduras. By Adolph Murie. (1935) Pp. 30, 1 plate, 1 map	\$0.35
No. 27.	The Birds of Northern Petén, Guatemala. By Josselyn Van Tyne. (1935) Pp. 46, 2 plates, 1 map	\$0.45
No. 28.	Fresh-Water Fishes Collected in British Honduras and Guatemala. By Carl L. Hubbs. (1935) Pp. 22, 4 plates, 1 map	\$0.25
No. 29.	A Contribution to a Knowledge of the Herpetology of a Portion of the Savanna Region of Central Petén, Guatemala. By L. C. Stuart. (1935) Pp. 56, 4 plates, 1 figure, 1 map	\$0.50

(CONTINUED ON LAST PAGES)

The publications of the Museum of Zoology, University of Michigan, consist of two series — the Occasional Papers and the Miscellaneous Publications. Both series were founded by Dr. Bryant Walker, Mr. Bradshaw H. Swales, and Dr. W. W. Newcomb.

The Occasional Papers, publication of which was begun in 1913, serve as a medium for original papers based principally upon the collections of the Museum. The papers are issued separately to libraries and specialists, and, when a sufficient number of pages has been printed to make a volume, a title page, table of contents, and index are supplied to libraries and individuals on the mailing list for the entire series.

The Miscellaneous Publications, which include papers on field and museum techniques, monographic studies, and other contributions not within the scope of the Occasional Papers, are published separately, and as it is not intended they will be grouped into volumes, each number has a title page and, when necessary, a table of contents.

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 81

**A Systematic Study
of the Avian Family Fringillidae
Based on the Structure
of the Skull**

BY

HARRISON B. TORDOFF

ANN ARBOR
UNIVERSITY OF MICHIGAN PRESS

APRIL 26, 1954

PRE FACE

IN spite of the relatively advanced state of avian taxonomy, relationships of certain groups, especially in the large order of perching birds, the Passeriformes, remain little understood today. Life-history studies have given important clues in many problems; other problems seem most apt to yield to morphological studies. This paper is a report on a study in the latter category.

Because of the comparatively poor representation of birds in fossil collections, the evolution of birds is not known in much detail. The strongly factual record presented, for example, to the mammalogist is lacking, and consequently ornithologists have been forced to draw the evolutionary picture of birds largely from inference based on Recent birds. This doubtless leads to many errors; yet in attempting to deduce from a study of modern birds the history of various groups, one gains some additional understanding of their relationships. I have felt justified, therefore, in presenting here certain hypothetical paths which may have been traveled in the evolution of the family Fringillidae.

This account of the skull structure and its significance in the family Fringillidae could never have been written without the willing assistance of many people. I am especially indebted to those listed below for the services indicated.

For collecting specimens for skeletons: Thomas D. Burleigh, Robert S. Butsch, Stephen W. Eaton, Ernest P. Edwards, Richard and Jean Graber, Charles O. Handley, Jr., William Heed, William A. Lunk, Paul S. Martin, Robert M. Mengel, Abelardo Moreno, Olin S. Pettingill, Jr., Allan R. Phillips, Haven H. Spencer, George M. Sutton, J. A. Weber, and J. Dan Webster.

For lending specimens in their care from the institutions indicated: Dean Amadon (American Museum of Natural History), Keith L. Dixon, Frank A. Pitelka, and Alden H. Miller (University of California Museum of Vertebrate Zoology), Herbert Friedmann (United States National Museum), and Robert W. Storer and Josselyn Van Tyne (University of Michigan Museum of Zoology).

For aiding in the tedious task of preparing skeletons for study: Jean Tordoff.

For making the drawings of skulls reproduced here: Jane S. Mengel.

For advice and technical aid in preparing the drawings for publication: William L. Brudon.

For friendly guidance and advice throughout this study: the members of my doctoral committee at the University of Michigan, Professors Claude W. Hibbard, Emmet T. Hooper, Alfred H. Stockard, George M. Sutton, and Charles F. Walker, and especially the chairman of that committee, Professor Josselyn Van Tyne. Dr. Robert W. Storer, of the University of Michigan, read an early draft of this paper and made several helpful suggestions.

CONTENTS

	Page
Introduction	7
The Skull in the Nine-Primaried Oscines	9
The Squamosal Region	9
The Bony Palate	10
The Fringillidae as an Artificial Group	13
The Relationship of the Carduelinae to the Fringillidae	14
Skeletal Characteristics	14
Zoogeographical Considerations	15
Migration	15
Habits	16
The Carduelinae as a Subfamily of the Ploceidae	18
Skeletal Characteristics	18
Zoogeography	19
Habits	19
Discussion	20
The New World Nine-Primaried Oscines	22
Skull Structure	22
Fringillinae	23
Geospizinae	24
Discussion	24
Special Problems in the New World Assemblage	28
A Proposed Classification for the Finches and Their Allies	32
Summary	33
Appendix: Forms Examined and Tabulation of Characters.	35
Literature Cited	40

ILLUSTRATIONS

Drawings of Skulls in Palatal View
(Figures 1-77 follow page 42)

Figures

1. *Spiza*, with important bones labeled.
- 2-9. *Dolichonyx*, *Agelaius*, *Icterus*, *Molothrus*, *Tersina*, *Diglossa*, *Chlorophanes*, *Icteria*.
- 10-17. *Passerina*, *Cyanocompsa*, *Guiraca*, *Pheucticus*, *Pyrrhuloxia*, *Richmondena*, *Rhodothraupis*, *Saltator*.
- 18-25. *Piranga*, *Chlorophonia*, *Habia*, *Chlorospingus*, *Melopyrrha*, *Tiaris*, *Geospiza*, *Pinaroloxias*.
- 26-33. *Fringilla*, *Melophus*, *Emberiza*, *Plectrophenax*, *Calcarius*, *Saltatricula*, *Embernagra*, *Poospiza*.
- 34-41. *Gubernatrix*, *Paroaria*, *Loxigilla*, *Sporophila*, *Oryzoborus*, *Atlapetes*, *Atlapetes*, *Arremonops*.
- 42-49. *Chlorura*, *Pipilo*, *Calamospiza*, *Passerculus*, *Ammodramus*, *Passerherbustus*, *Pooecetes*, *Chondestes*.
- 50-57. *Aimophila*, *Amphispiza*, *Junco*, *Spizella*, *Spizella*, *Zonotrichia*, *Passerella*, *Melospiza*.
- 58-65. *Bubalornis*, *Passer*, *Amblyospiza*, *Ploceus*, *Diatropura*, *Quelea*, *Steganura*, *Erythrura*.
- 66-73. *Amadina*, *Poephila*, *Mycerobas*, *Hesperiphona*, *Chloris*, *Carpodacus*, *Pinicola*, *Leucosticte*.
- 74-77. *Carduelis*, *Acanthis*, *Spinus*, *Loxia*.

A SYSTEMATIC STUDY OF THE AVIAN FAMILY FRINGILLIDAE,
BASED ON THE STRUCTURE OF THE SKULL*

INTRODUCTION

THIS is a study of the relationships of the avian family Fringillidae, order Passeriformes, based primarily on the structure of the skull. Two family categories used by recent authors, the Thraupidae and Ploceidae, which are closely allied to the Fringillidae, have also been included in this study. In addition, the remaining New World nine-primary Oscines are included in the classification proposed here; I have studied some in detail, others I have included largely on the basis of studies by other authors. Families in the latter category include Tersinidae, Vireonidae, Icteridae, Drepaniidae, Catamblyrhynchidae, Parulidae, and Coerebidae.

It has long been recognized that the Fringillidae are a diverse family, the sole distinguishing character of which is a strong tendency for the bill to be heavy and conical. It has been further recognized that heavy bills of the seed-eating type have been independently developed in several distinct phyletic lines. Examples are furnished by the cowbirds (*Molothrus*) and the Bobolink (*Dolichonyx oryzivorus*) of the Icteridae, *Psittirostra* of the Drepaniidae, and *Pyrrhuloxia* of the Thraupidae. In addition, the weaver finches (Ploceidae) are, as a group, as heavily-billed as the Fringillidae. No single external morphological feature as readily adaptable as the bill of birds is a satisfactory structure upon which to base taxonomic units of family rank.

The Fringillidae have been divided into as many as five subfamilies (Hellmayr, 1938:v): Geospizinae (see also Lack, 1947:13-14), Richmondinae, Emberizinae, Fringillinae, and Carduelinae. The divisions were based largely on the structure of the bony palate and the horny palate, as studied by Sushkin (1924, 1925). The divisions proposed by Sushkin were retained, although they were rearranged, in the American Ornithologists' Union Check-List, fourth edition (1931).

Many ornithologists have been dissatisfied with the classification of the Fringillidae as set forth in recent publications. Hellmayr's classification (1938) did not admit of the probability that *Saltator*, for example, is closer to the tanagers of the genus *Piranga* than to most other fringillids, but Sushkin (1924:38) stated that *Saltator* is a thick-billed tanager. Fifty years ago, Ridgway (1901:25) wrote that "the two supposed families [Fringillidae and Thraupidae] are clearly purely artificial." He wrote further that "this question as to whether the Fringillidae and Tanagridae [=Thraupidae] are really distinct family groups or not, and if they are, where the line between them should be drawn, is one which cannot now be exactly determined."

* Accepted for publication March 16, 1953.

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan.

Ridgway's pessimism was justified in 1901. Since then, however, collections have grown, and, more important, skeletons and alcoholic specimens have been preserved for anatomical dissection. In recent years, Beecher (1950) has given much attention to the phylogeny of the nine-primaried Oscines. He used the variations in the muscles of the jaws as the primary basis for his conclusions. Mayr and Amadon (1951) have recently proposed a radical rearrangement of the vireos, finches, tanagers, and allies. Their conclusions were influenced, at least in part, by Beecher's unpublished results, to which they had access.

In view of the foregoing, it is obvious that it is time to begin studies of various anatomical systems of the families of the Passeriformes, with the object of determining relationships on a family and subfamily level. I have chosen to analyze primarily the Fringillidae, using the skeletal system, for three reasons. First, this family has, as previously indicated, presented unusually complicated problems in attempts to define it and to ascertain its nearest relatives. Second, Sushkin's studies of fringillid skeletons, although fragmentary, seem to me to indicate a conservative and reliable approach to the problem at hand. Third, skeletons of birds of this and related families have become available in recent years in sufficient quantity to permit conclusive studies to be made.

As my study of the Fringillidae progressed, the problem proved larger than it originally appeared to be. It is impossible to restrict a study to a given recognized family when the family is an artificial group intergrading with other recognized families (as the Fringillidae do with the Thraupidae and the Ploceidae).

It became clear, finally, that the problem had become too large for adequate treatment as originally intended. Much would have been lost by disregarding families which are clearly involved in the broad picture of fringillid relationships. Accordingly, I decided to include all directly pertinent groups but to limit the study to an analysis of the variations of the skull, and especially of the bony palate. Many months of intensive study of the complete skeletons have convinced me that the characters of the bony palate are most useful systematically. The postcranial skeleton, on the other hand, is of much less use, except in delimiting the Carduelinae of the Fringillidae and the Ploceidae from the remaining groups (see pp. 14-15).

Some taxonomists regard their own line of research as providing the only solution for systematic problems. I realize that my conclusions may prove deficient in the light of evidence gathered in the future; however, since Sushkin's preliminary studies are the basis for most recent arrangements of the nine-primaried Oscines, it seems reasonable to continue the researches which he started. Especially is this true in view of the fact that my conclusions differ from those of Sushkin in several important respects.

For the sake of convenience I have used the family and subfamily names employed by Hellmayr (1935, 1936, 1937, 1938) in the discussions which follow. These names are familiar to most ornithologists

and are convenient for that reason. On pages 32-33, I have formally proposed an arrangement of family and subfamily names which seems to express relationships most satisfactorily, as based on my osteological studies and the work of other authors.

For the convenience of readers unfamiliar with Hellmayr's (1935, 1936, 1937, 1938) work, I have presented below a synopsis of his arrangement of the higher passerines. I have not studied the families which are here enclosed in brackets.

Family Vireonidae
 [Family Vireolaniidae]
 [Family Cyclarhidae]
 [Family Laniidae]
 [Family Sturnidae]
 Family Coerebidae
 Family Compsothlypidae (=Parulidae)
 Family Tersinidae
 Family Thraupidae
 Family Icteridae
 Family Ploceidae
 Family Catamblyrhynchidae
 Family Fringillidae
 Subfamily Richmondeninae
 Subfamily Geospizinae
 Subfamily Fringillinae
 Subfamily Carduelinae
 Subfamily Emberizinae

THE SKULL IN THE NINE-PRIMARYED OSCINES

Many features of the skull of birds have been mentioned by various authors as important to avian classification. I have already pointed out the disadvantages associated with placing undue emphasis on the shape of the bill. In the studies here reported I concluded that only two regions of the skull, the bony palate and the squamosal region, consistently offered characteristics useful in determining relationships at taxonomic levels above the genus in fringillids and their allies. The validity of the use of palatal structure for taxonomic purposes at the family level would seem at least inferentially justified by the wide use made of the palate in defining the orders of birds.

The Squamosal Region

The squamosal region varies mainly in amount of inflation. Many of the Emberizinae have expanded squamosals which often appear much like the auditory bullae of mammals. In the other groups treated here, the squamosal area is not inflated.

I do not know the significance of the varying amount of inflation of the squamosal region. It probably would be a rewarding subject for

investigation, especially in view of the similarity in this respect between the Fringillidae and certain rodents. In each group there is a definite tendency for the squamosal area (in the birds) or the auditory bullae (in the rodents) to be most inflated and enlarged in those forms which dwell in open country. There appears to be no unanimity of opinion among mammalogists regarding the significance of the enlarged bullae in mammals of the open country. It has been suggested that in rodents the inflation is associated with more acute hearing and/or better balance in open-country (and particularly saltatorial) kinds (Setzer, 1949:487-90), but in the case of birds little has been written on the subject of inflated squamosals. Beecher (1950:52) said merely that the squamosal area of the skull "is inflated in advanced buntings," whereas it is flattened in "primitive South American members" of the Emberizinae. Although it is true that inflation of the squamosal region is characteristic of many of the Emberizinae occurring in North America, and especially of those dwelling in open country, it seems desirable to point out here some facts which indicate that interpretation of the significance of the inflation is not to be undertaken lightly. First, although inflation of the squamosals seems to be correlated with life in open country, such strictly open-country genera as *Calcarius* and *Plectrophenax* have flattened squamosals, while *Zonotrichia*, species of which are typically dwellers in brushy or wooded areas, has squamosals which are much inflated in the region of the ear. Second, in regard to a possible saltatorial function, it should be pointed out that although the squamosal region is inflated in such genera as *Passerella* and *Pipilo*, both of which progress by hopping, it is equally inflated in *Passerherbulus* and *Ammodramus*, which progress, much of the time at least, by running.

In order fully to appreciate the comparison between rodents and fringillids drawn above, it would be necessary to know what structures are housed by the enlarged squamosal areas and auditory bullae and the function of those structures. I am not able to solve these problems at this time.

Regardless of the function of the inflation of the squamosal area of the skull, some use can be made of the amount of inflation in determining relationships, especially between genera.

The Bony Palate

I shall describe here only the two principal ways in which the bony palate of the nine-primaried Oscines differs from the generalized passeriform palatal structure (in which the prepalatine bars lack accessory projections and are not markedly broadened anteriorly).

First, in the New World nine-primaried Oscines (exclusive of the Carduelinae), a small bone frequently occurs as an accessory spur on each palatine. These spurs, the palato-maxillaries (Fig. 1), lie lateral and parallel to the prepalatine bars. Anteriorly, the spurs join with the premaxillary and the prepalatine bars; posteriorly they project into the space between the prepalatine bars and the jugals.

Palato-maxillaries are highly variable in those forms in which they do occur. They may be (1) relatively long (up to two-thirds or more of the palatines) and broad, as in *Pyrrhuloxia*; (2) long but relatively slender, as in *Tiaris*; (3) shortened and broad, as in *Saltator*; (4) completely free of the prepalatine bars except at the extreme anterior end, as in *Richmondia*; (5) closely approximated to the prepalatine bars but not fused, as in *Piranga*; or (6) fused more or less completely to the prepalatine bars, as in *Diuca*, *Spizella*, *Habia*, and many other genera.

Palato-maxillaries appear to be lacking in the great majority of passerine birds, and I have made the assumption here that the occurrence of palato-maxillaries in certain nine-primaried oscinine birds indicates a relationship among the forms possessing them. According to Amadon (1950:214): "Other investigators have reported... [palato-maxillaries] in a few families obviously not close allies of the Drepaniidae [and the other nine-primaried Oscines], namely, the Pycnonotidae, Hirundinidae, Dicaeidae, and Picidae." The significance of the occurrence of palato-maxillaries in the last four families is not known. Other evidence indicates that these families are far removed from the nine-primaried Oscines and, further, that they do not form a natural group in themselves. The Picidae, of course, are not even Passeriformes, but Piciformes. If structures which can be properly called palato-maxillaries do actually occur in the four families named by Amadon, it seems necessary to suggest that the structures have been independently developed in each of the four families. This, in turn, might reflect on the value of palato-maxillaries as an aid in determining relationships among birds. The occurrence, however, of palato-maxillaries in all species of certain groups of birds included in the present study makes it very probable that their presence reflects a common origin.

Amadon (1950:216) stated that "little is known of the significance [function?] of the palato-maxillaries." Accordingly, I have undertaken to determine the function of these bones through dissection of alcoholic specimens of species having palato-maxillaries free, partly fused to the prepalatine bars, fused, or absent.

A preliminary description of certain muscles of the jaw and of the roof of the mouth of birds is necessary in order to understand the function of the palato-maxillaries. The frontonasal hinge at the junction of the upper part of the bill and the frontal bones of a bird's skull is a well-known feature of the skull in birds. It is less generally understood, however, that this hinge permits a considerable amount of dorsoventral movement of the upper mandible in living birds. This movement is made possible through sliding of the footlike parts of the palatines and pterygoids along the rostrum (parasphenoid) of the cranium. The movement of the palate is in turn transmitted to the quadrate through the pterygoids and through the jugal and quadratojugal arch. The quadrate rocks in its double socket in the squamosal region, as required by the movements of the upper and lower jaw. (See Engels, 1940:363-66 and Beecher, 1951a:412-16, for excellent detailed discussions of the mechanics of palatal structure and associated musculature.)

According to Engels (1940:365), "the only muscle in passerine birds which acts to bring about the depression of the upper jaw is the pterygoideus [*M. pterygoideus* = *M. pterygoideus internus* of Shufeldt, 1890], except at the very end of the movement, when the posterior adductors of the lower jaw contribute slightly to the action." This is not completely true, however, since *M. pseudotemporalis profundus* (Beecher, 1951a:415) also depresses the upper jaw by retraction of the quadrate. The pterygoideus is the largest of the jaw muscles; it has its origin on the dorsal and ventral surfaces and the lateral borders of the palatines and over much of the pterygoids. Its insertion is made on the articular process of the lower jaw, its rostral face, and the adjacent part of the medial surface of the mandibular ramus. Often some lateral fibers pass over the ventral border of the posterior part of the lower jaw and insert on its lateral surface just below the articular area (described and figured in Engels, 1940:359).

From the foregoing discussion it should be clear that the pterygoideus is an important muscle in the "biting" action of the jaws of birds. Not only does it serve to depress the upper jaw, but through its insertion on the lower jaw it also is a definite factor in elevating the latter. With this description of the function of the palatal musculature in mind, it becomes possible to interpret the function of the palato-maxillaries. In those birds in which they are present and not fused to the prepalatine bars, a considerable part of the pterygoideus arises from the palato-maxillaries by means of strong tendinous attachments. In some birds the part of the pterygoideus arising from the palato-maxillaries is readily separable from the main body of the pterygoideus. In an adult male *Richmondena* I estimate that approximately 25 per cent of the entire mass of the muscle arises on the palato-maxillaries.

The palato-maxillaries, then, are an important additional area of origin for the pterygoideus. It thus seems reasonable to assume that palato-maxillaries were originally developed as a result of selective pressure for more effective action of the pterygoideus — stronger biting or squeezing action between the upper and lower jaw, a need ordinarily associated in passerine birds with the seed-eating habit. This important assumption will be discussed later.

In birds which have the palato-maxillaries fused to the prepalatine bars of the palatines, the part of the pterygoideus ordinarily arising on the palato-maxillaries arises instead on the lateral edge of the prepalatine bars. If the palato-maxillaries remain as flanges on the prepalatine bars, the pterygoideus arises in part from the posterior surface of the flanges. In any case, if the palato-maxillaries are fused, that part of the pterygoideus having its origin on them is reduced in bulk and presumably also reduced in effective action.

The second major departure (palato-maxillaries being the first) in the Fringillidae from the generalized passerine palatal structure occurs in the Carduelinae, in which the prepalatine bars are invariably flared anteriorly. This will be discussed later.

THE FRINGILLIDAE AS AN ARTIFICIAL GROUP

Modern systematists almost unanimously agree that the Fringillidae, as understood by such authorities as the American Ornithologists' Union Check-List Committee (1931), Hellmayr (1938), and Witherby and others (1938), are an artificial group, by no means of monophyletic origin. In spite of the general dissatisfaction, very few workers have attempted to analyze the family. Those who have set forth new or rearranged schemes of classification have, in my opinion, made serious errors.

The Fringillidae, as previously noted, usually have been divided into five subfamilies: Carduelinae, Fringillinae, Emberizinae, Geospizinae, and Richmondeninae. The five subfamilies, as will be shown later, can be reduced to three groups, not of equal rank, which, for convenience of discussion, may be named as follows: Carduelinae, Fringillinae (including Emberizinae and Geospizinae), and Richmondeninae. A clear-cut line, on osteological grounds, can be drawn between the Carduelinae and the two remaining subfamilies.

Mayr and Amadon (1951:28) said of the separation of the Fringillinae from the Carduelinae by Sushkin (1924:38): "He [Sushkin] gave no reason for this separation, and we think it unnecessary." My osteological studies make it evident that the Carduelinae are distinct from the Fringillinae (see discussion, pp. 23-24).

William Beecher (in personal letter, dated 21 June 1951) stated that, as a result of his studies of jaw musculature, he believes "the cardueline finches arise from the tanagers [family Thraupidae] and here the connecting forms are so close I cannot draw the line between the two families without being arbitrary." Beecher (1951b:279-80) indicated that the tanagers merge with the carduelines through the series *Piranga* — *Habia* — *Tanagra* — *Chlorophonia* — *Stephanophorus* — *Carpodacus*. I cannot state too strongly that this apparent intergradation between the tanagers and the carduelines in muscle pattern and horny palate is not confirmed by the bony palate. *Piranga* (Fig. 18), *Habia* (Fig. 20), *Tanagra*, *Chlorophonia* (Fig. 19), and *Stephanophorus* are, in palatal structure, all "good" tanagers; *Carpodacus* (Fig. 71) is typically cardueline. The similarities in jaw musculature and horny palate noted by Beecher must, in my opinion, be due to convergent development or to misinterpretation of the evidence.

Beecher (1951b:280) said that "plumage [color? pattern? structure?] generally supports the thesis of close relationship" of the carduelines to the tanagers. This seems to me to be misleading. The plumage may not deny a close relationship; still, in my opinion, it does not support such a relationship between these two groups. As a matter of fact, if the plumage were of any real help, the present problem probably would have been solved years ago.

To sum up, I have studied ample material of every New World cardueline genus, most of the Old World cardueline genera, and 26 genera of the Thraupidae, including representatives of every major grouping

of genera in the family. In none of these forms have I seen any osteological evidence of close affinity between the Carduelinae and the Thraupidae.

THE RELATIONSHIP OF THE CARDUELINAE TO THE FRINGILLIDAE

Skeletal Characteristics

The subfamily Carduelinae may be distinguished osteologically from the New World nine-primaried Oscines (hereinafter used as a general term to include only noncardueline forms) as follows:

Palatal structure.— All New World nine-primaried Oscines have palato-maxillaries, either free or fused to the prepalatine bars (see pp. 22-23 and Figs. 1-57); palato-maxillaries are lacking in carduelines, there being no trace of them even in fused form. In all Carduelinae the prepalatine bar is flared at its juncture with the premaxilla (Figs. 68-77), whereas the prepalatine bar in the noncardueline New World forms is not expanded anteriorly, or, if broadened anteriorly, does not have the characteristic lateral projection found in all Carduelinae. Of all New World forms, the prepalatine bars of *Oryzoborus* are broadest anteriorly. Yet Figure 38 shows clearly that in *Oryzoborus*, an extremely heavy-billed genus, the broad prepalatine bars do not have the lateral projection characteristic of carduelines. Amadon (1950:218) implied that the cardueline condition of the premaxilla-prepalatine articulation occurs in *Passerella* (Emberizinae), *Dolichonyx* (Icteridae), and "doubtless others" of the New World groups. This is incorrect (Figs. 2 and 56). The prepalatines frequently are broadened in adaptive response to the need of a strong, seed-crushing type of bill, but the cardueline condition is never achieved in noncardueline groups, with one apparent exception — certain genera of the Drepaniidae, to judge from the figures in Amadon's monograph, appear to have typically cardueline palates. This is undoubtedly the main reason for Sushkin's (1929) belief that the Drepaniidae were derived from cardueline stock. Amadon (1950) plausibly suggested that the presence of palato-maxillaries prevents expansion of prepalatine bars.

Squamosal region of skull.— Carduelines characteristically have flattened squamosals, although the same is true of many of the New World nine-primaried Oscines (see pp. 9-10, 28). The flattened squamosal region of the Carduelinae does, however, set them off from "the more advanced" North American forms among the Emberizinae. This is seemingly of little phylogenetic significance, inasmuch as the amount of inflation of the squamosal region seems useful taxonomically primarily at generic levels.

Humerus.— This bone in the Carduelinae is characterized by a proximal head that is broad in relation to its length. The ratios obtained by dividing the greatest width of the proximal head of the humerus by the length of the humerus are: Carduelinae, 0.33 — 0.36 (36

individuals, 11 species, 7 genera); Emberizinae, 0.27 - 0.33 (121 individuals, 36 species, 22 genera); Richmondinae, 0.30 - 0.33 (46 individuals, 10 species, 9 genera). Although there is no clear-cut separation between the subfamilies mentioned, it is interesting to note that the lowest ratio obtained for the Carduelinae (for *Leucosticte atrata*, a relatively sedentary cardueline species) is the same as the highest obtained for the Emberizinae (for *Plectrophenax nivalis*, perhaps the strongest flier of the North American Emberizinae). Short humeri with broad proximal heads are characteristic of strong-flying passerines; in view of this, the example just cited takes on added significance. As a group, however, the Carduelinae are stronger fliers and much more prone to long erratic movements than the New World finches. This alone could be responsible for the broadened and shortened humerus of the carduelines. In other words, the difference could be strictly adaptive and not of any phylogenetic significance.

Tarsometatarsus. — The Carduelinae have relatively short tarsometatarsi. The ratio obtained by dividing the length of the tarsometatarsus by the length of the sternum is as follows: Carduelinae, 0.67 - 0.92 (36 individuals, 11 species, 7 genera); Emberizinae, 0.81 - 1.31 (121 individuals, 36 species, 22 genera); Richmondinae, 0.82 - 1.04 (46 individuals, 10 species, 9 genera). Again, as in the ratios given above for the humerus, there is considerable overlap, but carduelines do tend to have a short tarsometatarsus and a correspondingly low tarsometatarsus-sternum ratio. The carduelines are more arboreal than the rest of the finches. Arboreal life as opposed to ground-living seems to result in shortened legs in many passerines. In the carduelines the femur and the tibiotarsus are also short, as compared with those of other finches, presumably also because of the arboreal existence of the former. The actual short-leggedness of the carduelines is familiar to all collectors.

Zoogeographical Considerations

Certain zoogeographical considerations support my thesis that the Carduelinae are not closely related to the New World nine-primaried Oscines, but are, instead, of Old World origin. Of the entire assemblage of carduelines, only two genera are endemic to the New World. One, *Loximitris*, is a monotypic West Indian genus closely allied to *Spinus* (Bond, 1950:170). The other, *Hesperiphona*, including only two species, is closely related to the Asiatic genera *Mycerobas* and *Eophona*. The distribution of *Hesperiphona*, namely, "western temperate North America, from British Provinces to the highlands of Guatemala" (Ridgway, 1901:38), points toward an Asiatic origin of the genus.

In contrast, the Old World has a total of at least ten endemic cardueline genera, with many endemic species.

Migration

The migration pattern of the North American fringillids points to an Old World origin for the carduelines. Perhaps the most regular

migrations among New World carduelines occur in the genus *Spinus*, which, judging by the large number of endemic species in Central and South America and its offshoot *Loximitris* in the West Indies, seems likely to have been the first cardueline genus to reach the New World. Even in *Spinus*, however, migrations are much less regular than in most Emberizinae and Richmondinae. The remainder of the New World carduelines are prone to erratic wanderings in the nonbreeding season. If the theory that the pattern of migration in New World birds was largely influenced by Pleistocene glaciation is correct, then the carduelines may well be considered to have arrived in North America sufficiently late in the Pleistocene that the pattern of migration was not so strongly influenced by glaciation (see Lincoln, 1950:8) as, for example, in the Emberizinae. This argument would not seem to apply to *Spinus*, however; the many peculiar forms developed by it and its fairly regular migrations indicate an earlier arrival in the New World than, at least, Middle Pleistocene. Most modern systematists agree that few, if any, species of Recent birds have evolved in the relatively short period from the Middle Pleistocene to the present. In order to accept the theory of a strong effect of glaciation on migration pattern, one must consider that the carduelines either were in North America throughout the Pleistocene and for some reason were not affected by glaciation in the same manner as other finches or that they arrived during the Pleistocene, having already developed in the Old World those species which are now endemic to the New World.

An alternative explanation of the erratic migration of the carduelines might be found in Stegmann's (1938, quoted from Mayr, 1946:33) belief that Old World birds, "developed for the most part in the always cold land mass of northern Siberia, . . . [are] so thoroughly adapted to the cold that . . . [they] can survive . . . [in temperate North America] without migration."

To sum up, the migration pattern of the New World carduelines is unlike that of the Emberizinae and the Richmondinae. It cannot, however, be said with certainty that the irregular migrations of the carduelines "prove" anything. They may be an adaptation to a particular type of food and perhaps represent no less advanced a condition than the more regular migrations of other finches. This utilization of unexploited food (various seeds, especially of conifers) by the carduelines may, to a large extent, be the reason for their successful invasion of the New World.

One fact remains — the carduelines are much less regularly migratory as a group than are the equally granivorous (in winter) emberizines and richmondines.

Habits

Many modern authors, especially in this country, have placed much emphasis on habits as a key to relationships. This is doubtless a healthy reaction to the earlier, purely morphological, basis for classification. But it must be remembered that adaptive convergence occurs in behavior, as well as in structure (Friedmann, 1946:395-98). For example, the significance of the nesting by the Tersinidae in holes in trees

(considered a remarkable family character by Mayr and Amadon, 1951:27) is somewhat diminished by the realization that at least some species of *Sicalis*, a South American fringilline genus, also utilize holes in trees for nesting.

With the appreciation of certain limitations of the usefulness of behavior traits in classification, I would like now to point out certain behavior patterns of the Carduelinae which seem, in my opinion, further to emphasize the gap between the Carduelinae and the New World finches.

The North American carduelines are more arboreal as a group than are the emberizines. They all possess flight songs, and this is more remarkable when one considers that none of the species (except in *Leucosticte* and occasionally in *Acanthis*) dwells in flat, treeless areas. Some Emberizinae also have flight songs, but they are forms dwelling in treeless plains, open fields, or tundra where elevated song perches are at a premium or lacking. Most richmondenines lack well-developed flight songs.

Dietary requirements are seldom, if ever, uniform throughout a polytypic family of birds. One item, however, in the diet of many North American carduelines is worth mentioning, namely, salt. Roberts (1936:377) noted the fondness for salt evinced by *Hesperiphona*, *Loxia curvirostra* and *L. leucoptera*, *Spinus pinus*, and *Carpodacus purpureus*. McCabe (1927:207) mentioned the attractiveness of salt as a bait for *Spinus pinus*, *Pinicola enucleator*, crossbills (*Loxia*), and, inferentially, redpolls (*Acanthis*). Aldrich (1939:172-73) described in detail the manner in which *Loxia curvirostra* eats salt, and he also noted that the crossbills were "occasionally accompanied by a few Cassin Purple Finches [*Carpodacus cassinii*] and Pine Siskins [*Spinus pinus*]" to the salt licks. Marshall (1940:219) corroborated Aldrich's (1939:172-73) observations and added *Hesperiphona* to his list of forms which eat salt. Peterson (1942:73) added *Carpodacus mexicanus*, *Spinus lawrencei*, and *Spinus psaltria* to the list of carduelines which eat salt. I have seen *Pinicola enucleator* eating dirt from freshly salted roads in New York. A few other passerines have been occasionally noted eating salt (*Passer domesticus*, *Corvus brachyrhynchos*, and probably others).

The carduelines thus differ markedly from other fringillids, which apparently do not eat salt. The physiological basis of salt-eating in birds has not been studied, but Van Tyne (verbal information) has suggested that salt-eating is correlated with a vegetarian diet. A similar correlation occurs in herbivorous mammals. One would infer that salt-eating is a trait in animals utilizing a diet with a low natural salt content; this seems to me only a partial answer, since the quantity of salt observed to be eaten by many carduelines appears to be far in excess of that which would be supplied by a carnivorous diet.

A more important trait of the Carduelinae lies in their nest sanitation, or better, their lack of nest sanitation. Among North American carduelines the nest is fouled with excreta by the young in *Spinus tristis*, *Spinus pinus* (Weaver and West, 1943:502; and Sutton, verbal information), and *Acanthis flammea*. Lawrence (1949:157) reported that both

Loxia curvirostra and *Carpodacus purpureus* left the "whole rim of the nest as well as the twigs around it . . . plastered with . . . [excreta] which the young had expelled over the border." Probably nest-fouling occurs but has not been reported in other North American carduelines. Also, Armstrong (1942:3) noted that the nest rim becomes deeply encrusted with excreta voided by nestling crossbills, *Loxia* (presumably the record refers to the Old World), although he attributed this lack of nest cleaning to the peculiar shape of the bill which renders the parents "unable to remove the excreta." Surely, this interpretation is wrong. Crossbills feed on tiny aphids at times, handling them with much dexterity. I have observed that a captive male *Loxia curvirostra* was fully capable of opposing the tips of the mandibles and thus manipulating small seeds with facility. So far as I know, all New World nine-primaried Oscines remove the excrement of the young throughout the nestling period.

An additional point (possibly of no great significance) is that the "Goldfinch [*Spinus*] and Purple Finch [*Carpodacus*], which belong to the subfamily Carduelinae, lay relatively smaller eggs than the Emberizinae" (Amadon, 1943:228).

THE CARDUELINAE AS A SUBFAMILY OF THE PLOCEIDAE

In view of the foregoing comments, I have concluded that the subfamily Carduelinae is not related to the New World nine-primaried Oscines. Instead, I think the carduelines are Old World in origin and closely related to the Ploceidae for the reasons given below.

Skeletal Characteristics

In palatal structure the Ploceidae show a steady progression from a generalized type with undilated prepalatine bars in the primitive *Bubalornis* up to a palate such as that of *Erythrura* or of *Poephila* (subfamily Estrildinae), which is practically identical with the typical cardueline palate (Figs. 58-67).

Many ploceids intermediate in palatal structure between *Bubalornis* and *Poephila* show a peculiar rotation of the prepalatine bars. Thus, in *Quelea* (subfamily Ploceinae) the prepalatine bars are twisted along their long axis in such a manner that the surface which is ventral at the junction of the prepalatine bar and premaxilla becomes, progressing posteriorly, lateral and finally dorsal (Fig. 63). The cardueline type of palate seems to have developed from stabilization and strengthening of this rotated palate, with the restriction of the prepalatine bar just behind the typical anterior expansion of the cardueline palate corresponding to that part of the prepalatine bar which is "on edge" in such forms as *Quelea*.

The Ploceidae do not seem, upon direct comparison, to differ materially from the Carduelinae in proportions of wing or leg bones, although I do not have series of ploceids available for measurement.

The squamosal region in ploceids is not inflated; this corresponds to the condition in the carduelines and many New World finches as well.

"In most passerine birds . . . the mediopalatine processes of the right and left palatine bones do not meet in the mid-ventral line for their full lengths. In ventral view the sphenoid rostrum is visible through the aperture between the two palatine processes. . . . In certain birds, principally heavy-billed finches, the mediopalatine processes meet or fuse completely beneath the rostrum. . . ." (Amadon, 1950:216). The latter condition is true of all cardueline finches, some Drepaniidae, and some ploceids (Amadon, 1950:217). Amadon further said that the same applies to "most or all of the Richmondinae (at least in the heavy-billed genera like *Sporophila*, *Richmondia*, and *Pheucticus*), and in a few of the heavier-billed Emberizinae like *Passerella*." I have not found that the mediopalatine processes are really fused (without a suture) in any emberizines or richmondines, although they sometimes are in close contact, separated by a distinct suture. For the present discussion, it is sufficient to point out that most (but not all) Estrildinae resemble the Carduelinae in this respect. This similarity may have no phylogenetic significance, but, instead, may be an example of adaptive convergence. As the number of similarities which must be assigned to "adaptive convergence" increases, however, one wonders if perhaps there is not a real phyletic relationship involved.

Zoogeography

In distribution the Ploceidae (exclusive of the Carduelinae) are Old World — if introductions by man are disregarded — being best represented in Africa, Asia, and Australia. The ploceids may be restricted in their Palearctic distribution by the wide adaptive radiation of the carduelines. Beecher thinks that the Carduelinae are derived from tanagers. If this is true, then it is necessary to consider that the carduelines reached the Palearctic ahead of the ploceids (assuming competition between the two groups), to account for their adaptive radiation there (Beecher, personal letter dated 21 June 1951). This complication is avoided if the Carduelinae are considered to be derived from the Ploceidae.

Habits

As previously stated about some Carduelinae, many kinds of ploceids leave the nest fouled by the excrement of the young. This would not seem to be an adaptively advantageous trait and may, perhaps, be taken as a further indication of close affinity between the two groups. Chapin (1917:267-79) listed the following ploceid genera in which at least some species do not clean the nest: *Amblyospiza* (Ploceinae), and *Spermestes*, *Nigrita*, *Clytospiza*, *Pytilia*, *Estrilda*, and *Poephila* (Estrildinae). (*Spermestes*, according to Delacour, 1943:85, is a synonym of *Lonchura*.) The habit may occur but be unreported in additional genera. It seems

significant to me that the Estrildinae, of all ploceids most like the Carduelinae morphologically, also share with the latter this peculiar habit of nest-fouling.

To those who will argue that the domed nests built by most ploceids preclude any close relationship to the carduelines, I should like to point out that domed nests frequently are an adaptation to existence in the tropics and occur in widely divergent groups. Thus, in a single garden in Jamaica, I have found globular nests with side entrances of the following kinds of birds: *Pyrrhuloxia jamaica*, *Coereba flaveola*, *Tiaris bicolor*, and *T. olivacea*. Though the three genera might be considered by some to belong to a single family, the amazingly close similarity of their nests (in contrast to others in the same family or families) seems to be an adaptive response to similar environmental conditions, rather than direct evidence of close relationship.

The Carduelinae, as a group, build the most compactly woven nests of any Fringillidae. This is not to be taken as direct evidence of cardueline-ploceid relationship. Yet the nests of the carduelines, in their structural complexity, are more like those of the ploceids than are the nests of the noncardueline fringillids.

Social instinct in the Ploceidae seems highly developed. Most ploceids are very gregarious during the nonbreeding season, and many kinds nest in compact colonies. In the Fringillidae, only the Carduelinae show, as a group, a comparable development of the social instinct. All North American carduelines, at least, usually form compact unified flocks in the nonbreeding season. Further, some carduelines actually nest in loose colonies (examples are *Spinus tristis*, *Carpodacus purpureus*, *Hesperiphona*, and *Loxia*). I consider this an important distinction between the carduelines and other fringillids. Colonial nesting and the flocking habit seem to emphasize the relationship shown in other ways between the carduelines and the ploceids.

Discussion

The sole external character used to separate the Ploceidae from the Carduelinae (and remaining fringillids) is the presence in the Ploceidae of a fairly well-developed tenth (outermost) primary and its apparent absence or vestigial condition in the Fringillidae. This distinction is by no means clear-cut; *Philetairus*, a ploceid genus in other respects, has a tiny, dorsally placed tenth primary, while in some fringillids, for example *Emberizoides*, the tenth primary is rather large and can be seen on the ventral surface of the wing (Chapin, 1917:253-54). In other families of passerine birds the tenth primary may be present in some species of a genus and absent in others (*Vireo* and *Dicaeum* are examples). In the higher passerine birds the tenth primary seems to be a disappearing structure. The taxonomic value of vestigial structures often is limited.

Mention should be made of Sushkin's (1924:37, 1925:256, 1927:1-2) discovery that certain species of *Montifringilla* (*alpicola* and *nivalis*)

and a few other supposed fringillids are actually ploceids. Sushkin and later authors (Witherby and others, 1938:153-54) placed *Montifringilla* in the ploceid subfamily Passerinae, with *Pyrgilauda*, *Onychostruthus*, *Passer*, *Petronia*, *Gymnoris*, and *Sorella*. Sushkin reached this decision after study of the horny palate of the forms involved. Some later authors, however, have misinterpreted Sushkin's intent. Sushkin intended that only *nivalis* and *alpicola* of *Montifringilla* be transferred to the Ploceidae. The remaining species of the genus (now in *Leucosticte*) he clearly stated were cardueline. But Witherby and his colleagues (1938:154) included in the statement of the geographic range of *Montifringilla* "a number [of species in]...North America." Obviously,

TABLE I

A Summary of Some of the Traits and Characteristics of the Finches
and of the Estrildinae, as Discussed in the Text

Abbreviations: p = present, a = absent, up = usually present, ua = usually absent,
NW = New World, OW = Old World.

		Richmondeninae	Emberizinae	Geospizinae	Fringillinae	Carduelinae	Estrildinae
Morphology	Palato-maxillaries (free or fused)	p	p	p	p	a	a
	Inflation of squamosal area	a	up	a	a	a	a
	Prepalatine bar with lateral projection	a	a	a	a	p	p
	Fused mediopalatine processes	a	a	a	a	p	up
	10th primary	p	ua	p	p	p	ua
Behavior	Salt-eating	a	a	a	a	p	?
	Nest-fouling	a	a	a	a	p(up?)	p(up?)
	Nest in colonies and/or strongly social in nonbreeding season	a	ua	a	a	p	p
	Well-developed flight song	ua	ua	a	up	p	p
Distribution	Greatest endemism of genera	NW	NW	NW	OW	OW	OW

Witherby and coauthors missed Sushkin's point, namely, that *Montifringilla* was an artificial group, only two species of which (including the genotype, *nivalis*) were ploceids. The North American species are typically cardueline, not ploceid. American authors have properly placed them in *Leucosticte*. The "finches" transferred by Sushkin to the Ploceidae are in the subfamily Passerinae. Osteologically, this group resembles the Carduelinae much less than do the Estrildinae.

I have found that *Poliospiza*, an African genus, perhaps also should be referred to the ploceid subfamily Passerinae. *Poliospiza* has been considered cardueline by recent authors, but the palatal structure of the single specimen (*P. leucopygia*) that I have seen is much like that of *Passer*. It is possible, of course, that the genus *Poliospiza* is an unnatural one; certain species may be cardueline, others ploceid. Neither *Passer* nor *Poliospiza leucopygia* shows any marked expansion anteriorly of the prepalatine bars; the prepalatine bars are not twisted or rotated in either (Fig. 59).

Sushkin (1924:38) believed that the "cardueline division is more closely related to the Ploceo-Passerine group than to the Emberizine," although he maintained the first two groups in separate families. Wolters (1949:11-16) placed the carduelines in the same family as the ploceids, but mistakenly united with the carduelines the forms placed by Sushkin and later authors in the Fringillinae and the Cardinalinae (=Richmondeninae). Wolters' studies are based on external morphology.

I think that the carduelines are ploceids, representing a further advance over the subfamily Estrildinae (according to Delacour, 1943:73, "the most advanced branch of the whole family Ploceidae"), to which they seem most related on the basis of palate structure and certain habits discussed above.

THE NEW WORLD NINE-PRIMARIED OSCINES

In this section I wish to discuss the relationships of the New World fringillid groups, which, however, cannot be considered alone. The family most nearly related to the New World finches is the Thraupidae, and these are considered here in some detail. Remaining families (as given by Hellmayr, 1935, 1936, 1937, 1938) in the New World nine-primaried assemblage are: Tersinidae, Vireonidae, Catamblyrhynchidae, Icteridae, Parulidae, and Coerebidae. An extralimital family, the Drepaniidae, has been shown by Amadon (1950), in a recent monograph of the family, to be related to this group of families.

Skull Structure

The regularity of occurrence of palato-maxillaries is a subject recently discussed by Amadon (1950:213-16) in some detail. He stated (p. 214) that "palato-maxillaries may be present in some species of a genus and absent in others," the statement apparently based on his

personal observations and on Lucas' (1894) work with coerebids and parulids. The quoted statement, if true, would cast serious doubt on the taxonomic value of the palato-maxillaries. But it is not true in any damaging way. Palato-maxillaries, once developed, are later lost only through fusion to the prepalatine bar. It is true that the degree of fusion does vary somewhat among species in a genus, or even among individuals in a single species. Yet this variation is not great. The palatal structure within a genus is much more uniform than Amadon implies.

Palato-maxillaries are relatively fragile bones; they are easily and frequently lost in preparation of skeletal material. If they are broken off it is difficult to see the original point of attachment. This possibility of accidental loss of the palato-maxillaries in preparation should be borne in mind when one is working with groups in which palato-maxillaries occur.

In the New World nine-primaried Oscines palato-maxillaries are present, either free or fused to the prepalatine bar, in the following groups: Parulidae, Coerebidae, Tersinidae, Thraupidae, Richmondeniinae, Emberizinae, Fringillinae, and Geospizinae. Palato-maxillaries are usually absent in adult Icteridae, Vireonidae, and Catamblyrhynchidae, but they probably were originally present and free, having since lost their identity through fusion in these families (see below). Amadon (1950:216) reported palato-maxillaries absent in the Drepaniidae; the affinities of the family (he thinks the family was derived from New World nine-primaried oscine ancestors) lead me to suggest that the palato-maxillaries were probably lost through fusion with the prepalatine bars in this family.

I have taken the actual or implied occurrence of palato-maxillaries in these families as an indication of their basic relationship, a relationship strongly suggested also on myological grounds (Beecher, MS) and on external characters. W. K. Parker (1878:253) said long ago that the presence of palato-maxillaries "suggests some delicate bond of affinity between the families where [they are] found." Shufeldt (1888) described and figured palato-maxillaries ("secondary palatine processes") in "*Habia* [= *Pheucticus*] *melanocephala*" and suggested that they warranted giving family rank to the genus. He also noted that *Piranga* somewhat resembled *Pheucticus* in skull structure. He thought this was an indication of their affinity.

Fringillinae

This subfamily was erected by Sushkin (1924) for the genus *Fringilla*, with its three species, *F. coelebs*, *F. montifringilla*, and *F. teydea*. Mayr and Amadon (1951:28), as previously noted, consider the Fringillinae not separable from the Carduelinae. It is true that in shape of bill and in color patterns this genus seems cardueline, yet the presence of short, sturdy palato-maxillaries, set off from the prepalatine bars by a distinct suture, indicates definite emberizine relationships. The lateral projection of the prepalatine bars, characteristic of carduelines, is

lacking in *Fringilla*. In palatal structure *Fringilla* may be considered a primitive emberizine (Fig. 26 and discussion, p. 28). If the Fringillinae are to be united with the Emberizinae, then the name Fringillinae should be maintained, rather than Emberizinae, since *Fringilla* is the type genus for the family Fringillidae.

Geospizinae

There is no necessity for retaining the geospizine finches (*Geospiza*, *Camarhynchus*, *Certhidea*, and *Pinaroloxias*, according to Lack, 1947:15) in a subfamily apart from the Fringillinae. They possess distinct palato-maxillaries which are more or less joined to the prepalatine bars, but always separated from the latter by definite sutures (Fig. 24). Mayr and Amadon (1951:38) included the Geospizinae in the Emberizinae.

Lack (1947:101) described what he considered to be the primitive external characters in Darwin's finches. He wrote (p. 101) that "though all the species [of Darwin's finches] show marked similarities to each other, they do not show a close resemblance to any particular species of finch on the South or Central American mainland. Either the mainland ancestor has become extinct, or Darwin's finches have diverged from it so far that their close relationship is no longer apparent." But Bond (1950:167) pointed out that "the Lesser Antillean genus *Melanospiza* bears a remarkable resemblance to *Geospiza*." I have not seen skeletons of *Melanospiza*, but it would seem logical to me that *Melanospiza* and Darwin's finches might have developed from the same primitive stock — now lost through extermination or evolution on the mainland — and might have been preserved through the protection offered them by insular existence (Darwin's finches occur only on the Galápagos Islands except for one species on Cocos Island). I consider Darwin's finches to be primitive Fringillinae, on the basis of palatal structure (see discussion below).

Discussion

There are two possible explanations of the occurrence of palato-maxillaries in the many groups listed above (p. 23). Either all forms have been derived from a common stock in which these bones were present, or palato-maxillaries have arisen independently a large number of times. In view of the absence of structures comparable to palato-maxillaries in other passerine birds (see p. 11), the second explanation must be rejected. There is abundant evidence, however, to indicate that loss of the palato-maxillaries through fusion to the prepalatine bars has taken place and is taking place (for reasons given below) in many now independent lines. As a result, I have been unable to work out any orderly scheme of arrangement of the various groups on the basis of palatal structure alone. Also, I have been unable to find definitive familial or subfamilial characters in the postcranial skeleton. Adaptive modifications in limb proportions and conformation of articular surfaces

of the bones have obscured actual phyletic relationships. These might well be clarified by sufficiently detailed anatomical studies, which are, however, outside the scope of the present problem.

Because I can give no satisfactorily detailed diagnosis of the various families and subfamilies involved, I have limited the following remarks to the hypothetical evolution of the New World nine-primaried Oscines, based on that factual material which seems pertinent. In the interests of nomenclatural stability, I have avoided suggesting any changes in the classification employed by Hellmayr (1935, 1936, 1937, 1938), except where the evidence makes such changes seem imperative.

In the introduction to this paper I gave reasons for believing that unfused palato-maxillaries are an adaptation to a diet of seeds or hard fruits, since their function seems to be to increase the effective action of the important pterygoideus muscle. If this assumption be granted, it follows that the ancestral stock of the New World nine-primaried Oscines (which, as shown above, almost certainly had unfused palato-maxillaries) was heavy-billed, probably seed-eating or at least adapted to a mixed diet.

From this stock the Richmondeninae were probably derived with little change in the basic palatal structure. It seems likely that the main change has been toward a heavier-billed condition, with consequent increase in size of the palato-maxillaries. *Richmondena* and *Pyrrhuloxia* (Figs. 14 and 15) represent the modern extreme in this development.

Certain tanagers such as *Piranga* (Fig. 18), *Chlorothraupis*, and *Phlogothraupis* show a tendency toward fusion of the palato-maxillaries. This is probably a reflection of a softer diet (insects and fruit) than that of the richmondenines. *Saltator* (Fig. 17) is somewhat closer to *Piranga* in palatal structure than to *Richmondena*, though it clearly is intermediate and thus shows the highly arbitrary nature of the widely accepted boundary between the Fringillidae and the Thraupidae. Sushkin (1924:38) and some others before him said *Saltator* was a thick-billed tanager; Ridgway (1901:24) and most subsequent authors have called *Saltator* a fringillid.

To return to the hypothetical ancestral stock, certain groups must have split off at an early time and become specialized for insect-feeding. As the need for extra strengthening of the bill diminished, the palato-maxillaries apparently shortened and fused with the prepalatine bars. The vireos, family Vireonidae, have the greatest reduction of palato-maxillaries; in Recent vireos the palato-maxillaries are no longer obvious. The former presence of palato-maxillaries in vireos would be entirely inferential were it not for the fact that a tiny separate splint of bone attached to the prepalatine bar persists in many Recent vireos.

Other groups which have lost or are now losing the palato-maxillaries are the Icteridae, Coerebidae, Parulidae, most Thraupidae, and Fringillinae. In the Icteridae (Figs. 2-5), the prepalatine bars often show a distinct flange in the region of the palato-maxillaries. That this flange represents fused palato-maxillaries is indicated by the following: in a juvenal *Quiscalus quiscula* (age 10-12 days) which I dissected, the

pterygoideus had a separate slip running to the flange; this flange, although partly ossified, was as yet not fused to the partly ossified prepalatine bar. Judging by its position and separate ossification, I concluded that the flange is an actual remnant of formerly distinct palato-maxillaries. Amadon (1950:216) and Parker (1878:266) have recorded indistinct and "well developed" palato-maxillaries, respectively, in the genus *Icterus*.

Beecher (1951b) has shown that the Coerebidae are an unnatural group. Three genera, *Coereba*, *Conirostrum*, and *Ateleodacnis*, are closely related to the Parulidae, but the remainder of the family Beecher considers to belong to the Thraupidae. In both the Parulidae and the Coerebidae (as understood by Hellmayr, 1935), palato-maxillaries are of frequent (probably regular) occurrence, although they are usually found fused to the prepalatine bars and set off from the latter only by rather indistinct sutures (Figs. 7-9). The universal tendency toward reduction and fusion of the palato-maxillaries in these families is again probably a reflection of a primarily insect or nectar diet.

I have already described the richmondenine-like condition of the palato-maxillaries in certain tanagers. Other genera in which the palato-maxillaries are similar to those of *Piranga* include *Compsocoma*, *Thraupis*, and *Ramphocelus*. In all remaining thraupid genera at hand the palato-maxillaries are thin and fused to the prepalatine bars. In all, however, sutures can be readily seen between the palato-maxillaries and the palatines. The tanagers not only merge with the Richmondeninae, as earlier described, but also seem to grade imperceptibly into the Fringillinae (see below). It does not seem probable, however, that the tanagers represent the stem stock from which the Richmondeninae developed on the one hand and the Fringillinae on the other, since modern tanagers lack the one supposed prerequisite of the hypothetical ancestors — namely, well-developed palato-maxillaries. In the tanagers, as in the vireos, warblers, honeycreepers, and blackbirds, the diet of soft foods (fruit and insects) is presumed to have caused (or permitted) loss of the palato-maxillaries.

In many ways the Fringillinae present the most instructive and most perplexing problem of all the New World groups. In the first place, the Fringillinae are largely seedeaters and relatively heavy-billed. This situation is supposed to favor well-developed palato-maxillaries, if the foregoing discussion has any validity. Yet, in practically all modern fringillines, the palato-maxillaries are nearly or completely fused to the prepalatine bars. To account for this, I can only postulate that the Fringillinae passed through a stage in their development wherein their primary adaptations were to a soft diet, probably insects. As a result, they lost well-developed palato-maxillaries, which were not regained when the fringillines later readapted to seeds. This speculation gains some credibility (though it is by no means proved) in the light of the following discussion of the subfamily.

In the Fringillinae of North America the palato-maxillaries normally are fused to the palatines. A single specimen of *Spizella pusilla* shows

unfused palato-maxillaries (Fig. 54). Since this occurred in only one of the many dozens of specimens examined, it seems likely that the lack of fusion represents an atavism; in "normal" fringillines of North America the unfused condition probably occurs only during early developmental stages. It is of interest to note that young fringillines often show less complete fusion of the palato-maxillaries than adults.

The hypothesis outlined above that the Fringillinae were insect-eaters at some earlier period is based on interpretation of morphological evidence. But this hypothesis gains some support from interpretation of zoogeographical evidence. To judge by the much greater distribution and wider adaptive radiation in North America of the Fringillinae, as compared with the Parulidae, Vireonidae, and Icteridae, it seems reasonable to suppose that the Fringillinae are an older group which reached North America, or, more likely, developed here, before the arrival of the insect-eating parulids, vireonids, and icterids. If this supposition is true, then we may suppose that the fringillines were exposed to a largely unexploited insect supply. Adaptation to this diet would have resulted in fusion of the palato-maxillaries; later, readaptation to seeds would result from the subsequent arrival of, and competition with, the highly efficient insect-eating warblers and vireos. Modern distribution of the warblers, vireos, and blackbirds indicates a South American or tropical North American origin for these groups (Mayr, 1946:21-22, 24).

Unfused palato-maxillaries are seemingly primitive in the Fringillinae; the present distribution of genera primitive in this respect is interesting. Palato-maxillaries which are unfused or incompletely fused are characteristic of the following fringilline genera: *Emberiza* (and its probably congeneric allies, *Fringillaria*, *Milaria*, and *Melophus*), *Fringilla*, *Calcarius* (including *Rhynchophanes*), *Plectrophenax*, *Geospiza*, *Camarhynchus*, *Certhidea*, *Pinaroloxias*, *Tiaris*, *Melopyrrha*, *Diuca*, *Saltatricula*, *Poospiza*, *Embernagra*, and *Emberizoides* (of the genera examined by me; see Figs. 22-33). The present distribution of these genera could scarcely be more remarkable; they occur in a ring at the periphery of the North American central land mass. The ring is interrupted only in oceanic areas where there are no islands to support terrestrial birds. *Emberiza* and *Fringilla* are palearctic (and the only primarily Old World fringillines); *Calcarius* and *Plectrophenax* are northern North American and panboreal; *Geospiza*, *Camarhynchus*, and *Certhidea* are restricted to the Galápagos; *Pinaroloxias* occurs only on Cocos Island; *Tiaris* and *Melopyrrha* are primarily West Indian (*Tiaris* occurs also in Mexico and Central and South America, and Bond, 1950:167, considers *Melanospiza*, also West Indian, closely allied to both *Tiaris* and *Geospiza*); *Diuca*, *Saltatricula*, *Poospiza*, *Embernagra*, and *Emberizoides* are South and Central American. This distributional pattern of the most primitive fringillines agrees closely with that which would be predicted as a result of Matthew's (1939) hypothesis concerning causes and methods of dispersal of animals. Matthew postulated that in the geographical distribution of major groups of mammals (and inferentially other kinds of animals) the large holarctic land masses

were the primary centers of dispersal, and the peripheral forms are most primitive or nearest to the ancestral type.

I have discussed earlier (pp. 9-10) the fact that the squamosal area is inflated in the advanced buntings. At this point I wish merely to point out that in the Fringillidae this tendency occurs only in the Fringillinae, and that, in general, there is a direct (though possibly coincidental) correlation between the amount of fusion of the palato-maxillaries and the amount of inflation of the squamosal region; that is, those genera showing the greatest amount of fusion (considered here to be an advanced character) of the palato-maxillaries also show the greatest inflation of the squamosal region. Thus, among the American fringillines occurring north of Mexico, only the genera *Calcarius* and *Plectrophenax* lack strongly inflated squamosals; in palatal structure also I consider these genera the most primitive (see above).

Investigation of the significance of large "auditory bullae" in birds would probably yield interesting results. Such genera as *Arremonops*, with the "bullae" little inflated in *verticalis*, more in *conirostris*, and most inflated in *rufivirgatus* would seem a logical group in which to start such an investigation.

Special Problems in the New World Assemblage

There is no convenient short term that can be used to include all of the New World nine-primaried Oscines. I trust that any reader realizes by this time that certain Old World genera (*Fringilla* and *Emberiza*) are included in the New World assemblage. I request the reader's indulgence in this ambiguity.

1. *Fringilla* and *Emberiza*.— These genera merit particular consideration, since they are the only fringilline genera endemic to the Old World. *Emberiza* has undergone much adaptive radiation there, having developed 28 or 29 species and at least three subgenera. *Emberiza* occurs in the palearctic, Ethiopian, and Indian regions. It is absent from Australia. *Fringilla*, on the other hand, contains only three species and is restricted to Europe, northwest Africa, Madeira, the Canaries, the Azores, and northern Asia (Witherby and others, 1938:102 and 110).

The palato-maxillaries in *Emberiza* are relatively longer than in *Fringilla*; in the former they are free at the tips, whereas they are fused throughout, but distinct and separated by a suture in the latter (Figs. 26 and 28). The primitive palate may be taken to indicate that these genera invaded the Old World at an early date, before a general fusion of the palato-maxillaries had taken place in the New World fringillines. Presumably, they then maintained a diet (seeds?) which did not permit further fusion. Further specialization for a diet of insects, such as apparently occurred in the New World, may have been prevented by competition with already established Old World insect-eaters, such as the family Muscicapidae. The more primitive palate, plus the greater adaptive radiation and wider distribution of *Emberiza*, seems to indicate that this genus or its ancestors arrived in the Old World before *Fringilla*.

2. Boundaries of the Richmondeninae.—As I have stated previously, I cannot define the various arbitrary groupings of the New World finches and allies on purely osteological grounds. If, however, *Gubernatrix*, *Paroaria*, *Porphyrospiza*, and *Tiaris* are considered fringilline, then the Richmondeninae (as given by Hellmayr, 1938:v) are uniform in that they all have well-developed palato-maxillaries, unfused for at least their posterior half. Various proposed classifications imply a close relationship between *Richmondena* and *Paroaria*, but osteological evidence does not bear this out (cf. Figs. 15 and 35).

Spiza is an aberrant member of this group in many ways (although not in palatal structure; see Fig. 1). Sushkin (1925:261) called it an "ancient, rather isolated genus... [of] very archaic, intermediate character." As a matter of opinion, I might suggest that *Spiza*, more than any other living genus, may give some insight into the nature of the hypothetical ancestor discussed above. Not only does *Spiza* meet the "requirements" in palatal structure, but its mixed diet, heavy bill, coloration (neither typically fringilline nor typically richmondenine), simple song, and distribution (eastern part of Great Plains area of North America) all correspond with the hypothetical attributes of the common ancestor.

Beecher (1951a:431), on the other hand, included *Spiza* in the Icteridae, "largely on the basis of jaw muscle pattern and the horny palate." He said: "Removal of this genus from the Emberizinae to the Icteridae is not so drastic since the latter have arisen from the former..." Beecher further wrote: "Since Hellmayr gave no reason for placing *Spiza* in the Richmondeninae, his divergence from the opinion [that *Spiza* is emberizine] of Ridgway and Sushkin is not to be taken seriously." Whether or not Hellmayr is to be taken seriously, he was surely correct in placing *Spiza* in the Richmondeninae if the bony palate is of any use taxonomically. *Spiza*, like the other Richmondeninae, has distinct, unfused palato-maxillaries. The Icteridae and the Emberizinae (of Beecher) resemble each other and differ from *Spiza* in that all of their genera lack distinct, unfused palato-maxillaries. I admit that *Spiza* is a peculiar genus in many ways, but its palatal structure is typically richmondenine.

Mayr and Amadon (1951) consider *Pyrrhuloxia* congeneric with *Richmondena* and, since *Pyrrhuloxia* is the older name, they call the subfamily Pyrrhuloxiinae. They are probably justified in uniting the genera, although many other fringillid genera are less well defined than *Pyrrhuloxia* and *Richmondena*, but I have followed the course here of retaining the familiar names *Richmondena* and Richmondeninae.

3. The Fringillinae-Thraupinae boundary.—I am unable to draw this boundary on osteological characters. In palatal structure the tanagers merge with the fringillines through such genera as *Habia* (Fig. 20), *Tachyphonus*, *Chlorospingus* (Fig. 21), *Cissopis*, *Phrygilus*, *Coryphospingus*, and others. The resemblance often goes further than pure morphology; Pitelka (personal letter dated 17 May 1951) noted from field observations that if *Chlorospingus* "is a tanager, then the border between

the fringillids and thraupids is indeed fuzzy... [*Chlorospingus* has the] notes and actions... of a sparrow... it appears to belong somewhere closer to *Arremonops*."

In this paper I have followed Hellmayr's (1938) allocation of genera to the Fringillinae (= Emberizinae plus Geospizinae and Fringillinae) with the following exceptions. *Porphyrospiza* and *Tiaris* should be transferred to the Fringillinae (near *Melanospiza*) from the Richmondeninae. *Paroaria* and *Gubernatrix* are fringilline, not richmondene, but I am uncertain of their relatives in the Fringillinae. Hellmayr included 15 genera in the Carduelinae which should be transferred to the Fringillinae. Mayr and Amadon (1951:28) thought they were largely richmondene. The incorrectly placed genera are: *Melanospiza*, *Loxipasser*, *Loxigilla*, *Melopyrrha*, *Piezorhina*, *Neorhynchus*, *Sporophila*, *Catamenia*, *Amaurospizopsis*, *Amaurospiza*, *Dolospingus*, *Oryzoborus*, *Volatinia*, *Gnathospiza*, and *Sicalis*.

4. Catamblyrhynchidae.— Mayr and Amadon (1951:27) made this family a subfamily of the Thraupidae. I have seen two skeletons of *Catamblyrhynchus diadema*, the only species in the family. The fact that palato-maxillaries are absent (presumably lost through fusion with the prepalatine bars) in these specimens seems to me to indicate that *Catamblyrhynchus* may have been derived from a fruit- or insect-eating ancestor, but I see nothing in its general palatal structure to indicate clearly its closest affinities. The anatomy of *Catamblyrhynchus* should be studied carefully to determine whether or not Mayr and Amadon are justified in placing this genus as a subfamily of the Thraupidae.

5. Tersinidae.— Lucas (1895) pointed out the peculiar palatal conformation of this monotypic family (Fig. 6). It agrees with other families here discussed in possessing short, distinct palato-maxillaries, but its peculiarities probably warrant its retention in a separate family. Lucas was most impressed by the "total absence of the transpalatine processes... I do not recall any other passerine in which the transpalatine process is totally absent."

6. Coerebidae.— Beecher (1951b:274-87) has shown convincingly that the family Coerebidae is an artificial group composed of nectar-adapted warblers (Parulidae) and nectar-adapted tanagers (Thraupidae) that have evolved convergently because of similarity of diet. To the impressive anatomical evidence given by Beecher in support of his opinion, I can add the following:

In *Coereba*, *Ateleodacnis*, and *Conirostris* the palato-maxillaries are absent—presumably they have fused to the prepalatine bars, and the sutures have become obliterated. These genera Beecher allocates to the Parulidae, a group in which fusion of the palato-maxillaries is characteristically far advanced.

Other coerebid genera which I have examined, *Chlorophanes*, *Cyanerpes*, *Dacnis*, and *Diglossa*, all show palato-maxillaries which, although fused to the prepalatine bars, are set off from the latter by more or less distinct sutures. These genera (and, according to Beecher, also *Iridophanes*, *Hemidacnis*, *Euneornis*, *Xenodacnis*, and *Oreomanes*) are

tanagers. The Thraupidae characteristically have much more distinct palato-maxillaries than the Parulidae.

I have retained the warbler "coerebids" in a separate subfamily, the Coerebinae, of the Parulidae. The tanager "coerebids" I have simply merged with the rest of the tanagers. Beecher (1951b:286-87) suggested the use of tribes, "Coerebini" for the warblers and "Dacnini" for the tanagers, to show the allocation of the nectar-adapted genera formerly placed in the Coerebidae.

7. Icteridae.— I readily admit the osteological resemblance of especially the heavier-billed icterids to many fringillids. However, the almost complete loss of the palato-maxillaries, with obliteration of the suture, the lack of inflation of the squamosal region of the skull even in advanced icterids, and the distinctive homogeneity of certain external morphological characteristics cause me to believe that the Icteridae are a phyletic unit apart from the Fringillinae. Beecher (1951a:411-40) thinks that the Icteridae have developed from an emberizine finch such as *Phrygilus* through primitive icterids such as *Molothrus*. The palatal structure of icterids seems neither to confirm nor to deny Beecher's theory.

8. The Fringillidae as a central stock.— Amadon (1950:232) stated that "a heavy, seed-crushing bill would seem to be something of an evolutionary dead end." He cited Darwin's finches as a possible exception but said: "It is by no means proved that the thinner-billed geospizids (*Certhidea* and, more especially *Pinaroloxias*) are not nearest the ancestral type." On the other hand, Bond (1950:167) contended that *Melanospiza*, a heavy-billed form, may be fairly close to the ancestral geospizine stock. Further, Lack (1947:101) specifically stated that strong evidence suggests that a heavy finchlike beak is a primitive geospizine feature. Amadon is correct in that it has not been "proved" that the ancestral geospizine was heavy-billed. Can such a matter ever be really proved?

If heavy bills are indeed evolutionary dead ends, then for a hypothetical ancestor of the fringillids, one must visualize some kind of bird with a bill at least as thin as the most needle-beaked living fringilline. By the same reasoning the ancestral crossbill (*Loxia*) must have been very thin-billed. If one grants that bills of seed-eating birds can become a little thinner, then it is fruitless to argue that they cannot become much thinner. I can see no justification for considering a heavy, seed-crushing bill an evolutionary dead end.

Wetmore (1940:2) expressed the idea here developed when he wrote: "The Fringillidae . . . [represent] the central group through which further progress may be expected. . . ." Glenny (1942:89), as a result of his studies of main arteries of the heart in fringillids, also concluded that "the Fringillidae probably represent a central group through which further evolution may be expected."

A PROPOSED CLASSIFICATION FOR THE FINCHES AND THEIR ALLIES

This study of the finches and their allies has led to certain changes in classification. I should emphasize here that these changes are desirable and necessary *on the basis of palatal structure*. Further studies may show that many conclusions expressed here must be modified or abandoned; however, I think that the major divisions as based on palatal structure are likely to prove to be natural groups. Some ornithologists may choose to consider the differences in the structure of the skull described in this paper as unimportant systematically. In the last analysis, there are probably few structural features of birds (or other animals) that are not "adaptive modifications." Therefore, it must be left to the judgment of each taxonomist to determine what modifications he considers of phylogenetic significance.

I here propose for the finches and their allies the following arrangement of families and subfamilies. The classification proposed by Mayr and Amadon (1951) is also presented for easy comparison by the reader.

Vireos, finches, and allies

Here proposed

- Family Vireonidae
- Family Icteridae
- Family Drepaniidae
- Family Catamblyrhynchidae
- Family Tersinidae
- Family Parulidae
 - Subfamily Coerebinae
(*Coereba*, *Conirostrum*,
Ateleodacnis)
 - Subfamily Parulinae
- Family Fringillidae
 - Subfamily Richmondeninae
 - Subfamily Thraupinae
(incl. "Coerebidae," less
Coereba, *Conirostrum*,
and *Ateleodacnis*)
 - Subfamily Fringillinae

Mayr and Amadon

- Family Vireonidae
- Family Drepaniidae
- Family Thraupidae
 - Subfamily Parulinae
 - Subfamily Coerebinae
 - Subfamily Catamblyrhynchinae
 - Subfamily Thraupinae
 - Subfamily Pyrrhuloxiinae
[=Richmondeninae]
- Family Tersinidae
- Family Fringillidae
 - Subfamily Emberizinae
 - Subfamily Fringillinae
[= Carduelinae plus
Fringilla]
- Family Icteridae

Weaverbirds, linnets, etc.

- Family Ploceidae
 - Subfamily Bubalornithinae
 - Subfamily Passerinae
 - Subfamily Ploceinae
 - Subfamily Viduinae
 - Subfamily Estrildinae
 - Subfamily Carduelinae

- Family Ploceidae
 - Subfamily Bubalornithinae
 - Subfamily Passerinae
 - Subfamily Ploceinae
 - Subfamily Viduinae
 - Subfamily Estrildinae

This arrangement seems, on the whole, to express satisfactorily the relationships at the family and subfamily level. Much more work is necessary, however, to delimit adequately and characterize the subfamilies Fringillinae, Thraupinae, and Richmondinae.

In contrast to Mayr and Amadon, I prefer to maintain the Parulinae and the Coerebinae in a separate family, the Parulidae. I admit, however, that the warblers and honeycreepers are related to the rest of the New World nine-primaried Oscines. The difference arises from difficulty in evaluating "family" characters. The main purpose served by my more conservative classification may be convenience.

SUMMARY

A study of the skeleton, particularly of certain characters of the skull, in the avian family Fringillidae provides a new basis for a review of the relationships of this family and its allies.

The birds now grouped under the family name Fringillidae have previously been characterized solely by a heavy conical bill. The bill of passeriform birds is a readily adaptable structure and is not consistently reliable as a taxonomic character at family level. In the present study the bony palate and the squamosal region of the skull were found to be conservative characters; the former useful in ascertaining family and subfamily relationships, the latter in showing relationships within the subfamily Fringillinae, as defined in this paper.

In the Fringillinae, the squamosal region varies mainly in amount of inflation. A positive correlation seems to exist in these birds between amount of inflation of the squamosal region and open-country habitat. There is no apparent correlation between inflation of the squamosal region and habits (such as method of locomotion on the ground). The greatest inflation of the squamosal region occurs in the supposedly most advanced members of the Fringillinae, namely, those living in North America.

Two variations of the bony palate are important to this study. First, palato-maxillaries occur in the New World nine-primaried Oscines. Palato-maxillaries, present in nine-primaried Oscines, are absent in most (as strict homologues, perhaps in all) other Passeriformes. The universal occurrence — either functional or vestigial — of these bones in the nine-primaried Oscines is here taken to indicate a common origin for the group. Second, the prepalatine bars of the Carduelinae and Estrildinae are markedly broadened anteriorly and bear a lateral projection. This morphological similarity between the two groups — together with other shared traits mentioned below — is here interpreted as indicating phylogenetic relationship.

The Carduelinae can be separated from the remaining Fringillidae in palatal structure, proportions of the humerus and leg bones, certain dietary requirements, distribution, migration habits, singing habits,

social behavior, and nest sanitation. Most points in which the Carduelinae differ from other fringillids are those in which the former resemble the Estrildinae of the Ploceidae. It seems reasonable to conclude that the carduelines are ploceids.

In the Fringillidae (*sensu stricto*), three subfamily groupings seem necessary: the Fringillinae, the Richmondinae, and the Thraupinae. The Fringillinae include the Geospizinae, Emberizinae, and Fringillinae of most recent authors, which can be united on the basis of palatal structure and other similarities. The Richmondinae, as here defined, correspond (with the exception of four genera transferred to the Fringillinae) to the Richmondinae of Hellmayr (1938:v). Richmondines uniformly possess well-developed palato-maxillaries, free from the prepalatine bars for at least their posterior half. Both the Fringillinae and the Richmondinae merge in palatal structure and external morphology with certain genera of tanagers (Thraupidae of most authors). For this reason the tanagers are here included in the Fringillidae as the subfamily Thraupinae.

Most variations in palatal structure seem connected, functionally, with diet. With this premise as a starting point, a hypothetical evolutionary course has been traced for the New World nine-primaried Oscines.

APPENDIX: FORMS EXAMINED
AND TABULATION OF CHARACTERS

I have appended here an alphabetical list of genera and species, arranged by families, which I examined osteologically in the present study. Following each generic name (or following specific names where my material shows marked intrageneric variation) are abbreviations showing the type of the palate and the degree of inflation of the squamosal area. The last number after each specific name is the number of skeletal specimens I examined of that species.

The meaning of each abbreviation is given here:

For all families listed:

Squamosal region not inflated	S1
Squamosal region slightly inflated	S2
Squamosal region much inflated	S3

For New World groups only:

Palato-maxillaries free of prepalatine bars for one-half or more of their length	Pa1
Palato-maxillaries adjacent to, but not closely fused with, prepalatine bars for most of their length	Pa2
Palato-maxillaries fused for most or all of length; suture present.	Pa3
Palato-maxillaries completely fused; suture not evident	Pa4

For family Ploceidae only:

Prepalatines generalized (i.e., neither twisted nor expanded anteriorly with lateral projection)	Pr1
Prepalatines twisted or rotated	Pr2
Prepalatines expanded anteriorly with lateral projection.	Pr3

VIREONIDAE

<i>Vireo</i> S1, Pa3 or 4
<i>bellii</i> 5
<i>flavifrons</i> 5
<i>gilvus</i> 5
<i>griseus</i> 5
<i>huttoni</i> 3
<i>olivaceus</i> 5
<i>solitarius</i> 5

Dolichonyx S1, Pa4 (or 3, rarely)

<i>oryzivorus</i> 5
<i>Euphagus</i> S1, Pa4 or 3
<i>cycnocephalus</i> 5
<i>Gymnostinops</i> S1, Pa4
<i>montezuma</i> 5
<i>Icterus</i> S1, Pa3 or 4
<i>bullockii</i> 5
<i>galbula</i> 5
<i>gularis</i> 3
<i>mesomelas</i> 1
<i>pustulatus</i> 2
<i>spurius</i> 5

ICTERIDAE

<i>Agelaius</i> S1, Pa4
<i>phoeniceus</i> 5
<i>Amblycercus</i> S1, Pa4
<i>holosericeus</i> 1
<i>Cassidix</i> S1, Pa4
<i>melanicterus</i> 1
<i>Cassidix</i> S1, Pa4 (or 3, rarely)
<i>mexicanus</i> 5
<i>Dives</i> S1, Pa4
<i>dives</i> 1

<i>Molothrus</i> S1, Pa4
<i>ater</i> 5
<i>Quiscalus</i> S1, Pa4 or 3
<i>quiscula</i> 5
<i>Sturnella</i> S1, Pa4
<i>magna</i> 5
<i>neglecta</i> 5

Tangavius S1, Pa4
aeneus 5
Xanthocephalus S1, Pa4 (or 3, rarely)
xanthocephalus 5

CATAMBLYRHYNCHIDAE

Catamblyrhynchus S1, Pa4
diadema 2

TERSINIDAE

Tersina S1, Pa3
viridis 1

PARULIDAE

Subfamily Coerebinae

Ateleodacnis S1, Pa4
bicolor 4
Coereba S1, Pa4
flaveola 6
Conirostrum S1, Pa4
albifrons 1
rufum 1

Subfamily Parulinae

Dendroica S1, Pa4
coronata 5
petechia 5
Geothlypis S1, Pa4 (or 3, rarely)
trichas 5
Icteria S1, Pa3
virans 5
Mniotilta S1, Pa4
varia 5
Oporornis S1, Pa3 or 4
formosus 5
Parula S1, Pa4
americana 5
Protonotaria S1, Pa3 or 4
citrea 4
Seiurus S1, Pa3 or 4
aurocapillus 5
Setophaga S1, Pa3 or 4
ruticilla 5
Vermivora S1, Pa4 (or 3, rarely)
peregrina 5
Wilsonia S1, Pa3 or 4
pusilla 5

FRINGILLIDAE

Subfamily Richmondininae

Caryothraustes S1, Pa1
poliogaster 1
Cyanocompsa S1, Pa1
parellina 3
Guiraca S1, Pa1
caerulea 10
Passerina S1, Pa1
amoena 3
ciris 4
cyanea 7

Pheucticus S1, Pa1
ludovicianus 6
melanocephalus 6
Pyrrhuloxia S1, Pa1
sinuata 5
Rhodothraupis S1, Pa1
celaeno 4
Richmondia S1, Pa1
cardinalis 20
Saltator S1, Pa2 or 3
atriceps 4
maximus 2
Spiza S1, Pa1
americana 20

Subfamily Thraupinae

Calospiza S1, Pa3 (or 2, rarely)
arthus 1
cayana 1
chrysophrys 1
cyanoptera 3
dowii 1
florida 2
gyrola 1
icterocephala 2
nigro-cincta 7
ruficapilla 1
Chlorophanes S1, Pa3
spiza 6
Chlorophonia S1, Pa3
occipitalis 4
Chlorospingus S1, Pa3 or 4
ophthalmicus 2
pileatus 2
Chlorothraupis S1, Pa2 or 3
carmioli 1
olivacea 1
Cissopis S1, Pa3
leveriana 4
Compsocoma S1, Pa3
flavinucha 1
Cyanerpes S1, Pa3
cyaneus 1
Cypsnagra S1, Pa3
hirundinacea 1
Dacnis S1, Pa3
venusta 3
Diglossa S1 or 2, Pa3
baritula 2
Habia S1, Pa3
gutturalis 7
rubica 4
Hemispingus S1, Pa3
superciliaris 1
Hemithraupis S1, Pa3
flavicollis 1
Nemosia S1, Pa3
pileata 3
Nesospingus S1, Pa3
speculiferus 1
Phaenicophilus S1, Pa3 or 4
palmarum 4

- Phlogothraupis* S1, Pa3
sanguinolenta 1
Piranga S1, Pa2 or 3
bidentata 2
flava 4
ludoviciana 4
olivacea 5
rubra 5
Poecilothraupis S1, Pa3
lacrymosa 1
Pyrrhuloxia S1, Pa3
jamaica 2
Ramphocelus S1, Pa3
dimidiatus 1
passerinii 3
Schistoclamys S1, Pa3
ruficapillus 1
melanopsis 3
Spindalis S1, Pa3
zena 2
Stephanophorus S1, Pa2 or 3
diadematus 2
Tachyphonus S1, Pa3
delatrii 1
luctuosus 1
rufus 4
Tanagra S1, Pa3
affinis 4
anneae 6
gouldii 1
lauta 3
Tanagrella S1, Pa3
velia 2
Thraupis S1, Pa3
abbas 10
episcopus 8
palmarum 1
Trichothraupis S1, Pa3
melanops 1
 Subfamily Fringillinae
Aimophila S3, Pa4 (or 3, rarely)
botteri 1
cassini 6
humeralis 1
rufescens 3
ruficauda 1
Ammodramus S1, Pa4 (or 3, rarely)
savannarum 6
Amphispiza S1, Pa4
bellii 3
bilineata 3
Arremon S2-3, Pa3 or 4
aurantiostrius 2
Arremonops
conirostris S2-3, Pa3 or 4; 3
rufivirgatus S3, Pa3 or 4; 8
verticalis S2, Pa3; 1
Atlapetes S2, Pa3 or 4
brunnei-nucha 1
torquatus 1
pileatus 1
Brachyospiza S3, Pa3 or 4
capensis 4
Calamospiza S3, Pa4
melanocorys 6
Calcarius S1, Pa3
lapponicus 10
ornatus 3
Camarhynchus S1, Pa3
parvulus 1
Catamenia S1, Pa3 or 4
analis 2
Certhidea S1, Pa3
olivacea 1
Chlorura S3, Pa3 or 4
chlorura 6
Chondestes S3, Pa4 (or 3, rarely)
grammacus 6
Coryphospingus S2, Pa3 or 4
cucullatus 3
pileatus 2
Diuca S1, Pa3 (or 2?)
diuca 4
Emberiza S2 or 3, Pa3
calandra S2; 2
cirlus S2; 2
citrinella S3; 3
Emberizoides S1, Pa3 or 4
herbicola 1
Embernagra S1, Pa3 or 4.
platensis 2
Fringilla S1, Pa3
coelebs 7
montifringilla 1
Fringillaria S1, Pa? (damaged)
impetuani 1
Geospiza S1, Pa3
conirostris 4
fortis 4
fuliginosa 4
magnirostris 4
scandens 4
Gubernatrix S1, Pa3 or 4
cristata 2
Junco S3, Pa4
hyemalis 6
oreganus 5
phaenotus 2
vulcani 3
Lophospingus S1, Pa3 or 4
pusillus 3
Loxigilla S1, Pa4
violacea 2
Melophus S1, Pa3
lathamii 1
Melopyrrha S1, Pa1 or 2
nigra 5
Melospiza S3, Pa4 (or 3, rarely)
georgiana 6
lincolni 6
melodia 6

Melospiza S3, Pa3 or 4
 kieneri 4
Myospiza S2-3, Pa3 or 4
 humeralis 4
Oriturus S3, Pa3 or 4
 superciliosus 2
Oryzoborus S1, Pa4
 angolensis 1
 crassirostris 1
Paroaria S1, Pa3 or 4
 coronata 6
 dominicana 2
Passerculus S3, Pa4 (or 3, rarely)
 princeps 1
 sandwichensis 6
Passerella S3, Pa4 (or 3, rarely)
 iliaca 10
Passerherbulus S3, Pa4 (or 3, rarely)
 caudacutus 4
 henslowii 4
Pezopetes S2-3, Pa3
 capitalis 1
Phrygilus S1-2, Pa3 or 4
 alaudinus 1
 carbonarius 1
 fruticeti 2
Pinaroloxias S1, Pa3
 inornata 4
Pipilo S3, Pa4 (or 3?)
 erythrophthalmus 6
 fuscus 4
 maculatus 6
 ocai 3
Plectrophenax S1, Pa3
 nivalis 8
Poocetes S3, Pa4 (or 3, rarely)
 gramineus 6
Poospiza S1-2, Pa3 or 4
 melanoleuca 1
 ornata 1
 torquata 1
Porphyrospiza S1, Pa3
 caerulescens 1
Pselliophorus S2-3, Pa3
 tibialis 1
Rhynchophanes S1, Pa3
 mccownii 4
Saltatricula S2, Pa3
 multicolor 1
Sicalis S1, Pa4 (or 3, rarely)
 flaveola 2
 luteola 2
Spizella S3, Pa4, 3, or, rarely, 2
 arborea 5
 passerina 5
 pusilla 53
Sporophila S1, Pa4
 aurita 4
 minuta 4
 torqueola 4

Tiaris S1, Pa1 or 3
 canora Pa1; 3
 olivacea Pa3; 4
Volatinia S1, Pa3
 jacarina 6
Zonotrichia S1, Pa3 or 4
 albicollis 6
 leucophrys 4
 querula 6

PLOCEIDAE

Subfamily Bubalornithinae

Bubalornis S1, Pr1
 albirostris 1

Subfamily Passerinae

Passer S1, Pr1
 domesticus 6
Poliospiza S1, Pr1
 leucopygia 1

Subfamily Ploceinae

Amblyospiza S1, Pr1 (expanded as in
Oryzoborus, not Carduelinae)

albifrons 1
Coliuspasser S1, Pr2
 eques 1

Diatropura S1, Pr2
 procne 1

Euplectes S1, Pr2
 hordacea 1

Foudia S1, Pr2
 madagascariensis 1

Hyphanturgus S1, Pr1-2
 nigricollis 1

Malimbus S1, Pr1
 malimbicus 1

Ploceus S1, Pr2
 cucullatus 3

rubiginosus 1

Quelea S1, Pr2
 sanguirostris 1

Sporopipes S1, Pr2
 frontalis 1

Symplectes S1, Pr1
 amaurocephalus 1

Subfamily Viduinae

Hypochera S1, Pr2
 chalybeata 1

Steganura S1, Pr2
 paradisaea 2

Vidua S1, Pr2
 macroura 1

Subfamily Estrildinae

Amadina S1, Pr2-3
 fasciata 1

Clytospiza S1, Pr2
 monteiri 1

Erythrura S1, Pr3
 psittacea 1

- Estrilda* S1, Pr2-3
 amandava 1
 angolensis 1
 coerulescens 1
 melpoda 1
Lonchura S1, Pr2-3
 bicolor 1
 cucullata 1
 malabarica 1
 molucca 1
Nigrita S1, Pr2
 canicapilla 1
Parmoptila S1, Pr1 (slightly 2?)
 woodhousei 1
Pirenestes S1, Pr3 (slightly 2)
 ostrinus 1
Poephila S1, Pr3 (slightly 2)
 annulosa 1
 gouldiae 1
 guttata 12
 phaeton 1
Spermophaga S1, Pr2-3
 haematina 1
Zonaeginthus S1, Pr2-3
 pictus 1
 Subfamily Carduelinae
Acanthis S1, Pr3
 cannabina 5
 flammea 8
 flavirostris 2
Callacanthis S1, Pr3
 burtoni 1
Carduelis S1, Pr3
 carduelis 7
Carpodacus S1, Pr3
 mexicanus 6
 purpureus 8
Chloris S1, Pr3
 chloris 3
 Coccothraustes S1, Pr3
 coccothraustes 3
Eophona S1, Pr3
 melanura 5
Fringilla S1, Pr3
 nemoricola 1
Hesperiphona S1, Pr3
 abeillii 1
 vespertina 12
Leucosticte S1, Pr3
 atrata 3
 lephrocotis 4
Linurgus S1, Pr3
 olivaceus 1
Loxia S1, Pr3
 curvirostra 10
 leucoptera 3
Loximitris S1, Pr3
 dominicensis 2
Mycerobas S1, Pr3
 melanoxanthus 3
Perissospiza S1, Pr3
 carnipes 2
Pinicola S1, Pr3
 enucleator 4
Pyrrhula S1, Pr3
 erythaca 4
 pyrrhula 1
Rhodospiza S1, Pr3
 obsoleta 2
Serinus S1, Pr3
 canarius 6
Spinus S1, Pr3
 pinus 5
 psaltria 1
 spinus 3
 tristis 9
 xanthogaster 2

LITERATURE CITED

- Aldrich, Elmer C.
1939 Notes on the Salt-feeding Habits of the Red Crossbill. *Condor*, 41:172-73.
- Amadon, Dean
1943 Bird Weights and Egg Weights. *Auk*, 60:221-34.
1950 The Hawaiian Honeycreepers (Aves, Drepaniidae). *Bull. Amer. Mus. Nat. Hist.*, 95:151-262.
- American Ornithologists' Union
1931 Check-List of North American Birds. 4th ed.; Lancaster, Pa.: Amer. Ornithol. Union.
- Armstrong, Edward A.
1942 *Bird Display*. Cambridge, England: Cambridge Univ. Press.
- Beecher, William J.
1950 Convergent Evolution in the American Orioles. *Wilson Bull.*, 62:51-86.
1951a Adaptations for Food-getting in the American Blackbirds. *Auk*, 68:411-40.
1951b Convergence in the Coerebidae. *Wilson Bull.*, 63:274-87.
- Bond, James
1950 Check-List of the Birds of the West Indies. 3d. ed.; Acad. Nat. Sci. Phila.
- Chapin, James P.
1917 The Classification of the Weaver-birds. *Bull. Amer. Mus. Nat. Hist.*, 37:243-80.
- Delacour, Jean
1943 A Revision of the Subfamily Estrildinae of the Family Ploceidae. *Zoologica*, 28:69-86.
- Engels, William L.
1940 Structural Adaptations in Thrashers (Mimidae; Genus *Toxostoma*) with Comments on Interspecific Relationships. *Univ. Calif. Publ. Zool.*, 42:341-400.
- Friedmann, Herbert
1946 Ecological Counterparts in Birds. *Sci. Mo.*, 43:395-98.
- Glenny, Fred H.
1942 A Systematic Study of the Main Arteries in the Region of the Heart — Aves — III. The Fringillidae. Part 1. *Ohio Journ. Sci.*, 42, No. 2:84-90.
- Hellmayr, Charles E.
1935 Catalogue of Birds of the Americas. *Field Mus. Nat. Hist., Zool. Ser.*, 13, pt. 8.
1936 Catalogue of Birds of the Americas. *Ibid.*, 13, Pt. 9.
1937 Catalogue of Birds of the Americas. *Ibid.*, 13, Pt. 10.
1938 Catalogue of Birds of the Americas. *Ibid.*, 13, Pt. 11.
- Lack, David
1947 *Darwin's Finches*. Cambridge, England: Cambridge Univ. Press.
- Lawrence, Louise de Kiriline
1949 The Red Crossbill at Pimisi Bay, Ontario. *Canadian Field-Nat.*, 63:147-60.
- Lincoln, Frederick C.
1950 Migration of Birds. U. S. Fish and Wildlife Serv., Circular 16.
- Lucas, Frederic A.
1894 Notes on the Anatomy and Affinities of the Coerebidae and Other American Birds. *Proc. U. S. Natl. Mus.*, 17:299-312.
1895 Osteological and Pterylographical Characters of the Procnatiidae. *Ibid.*, 18:505-7.
- McCabe, T. T.
1927 Bird Banding near Barkerville, British Columbia. *Condor*, 29:206-7.

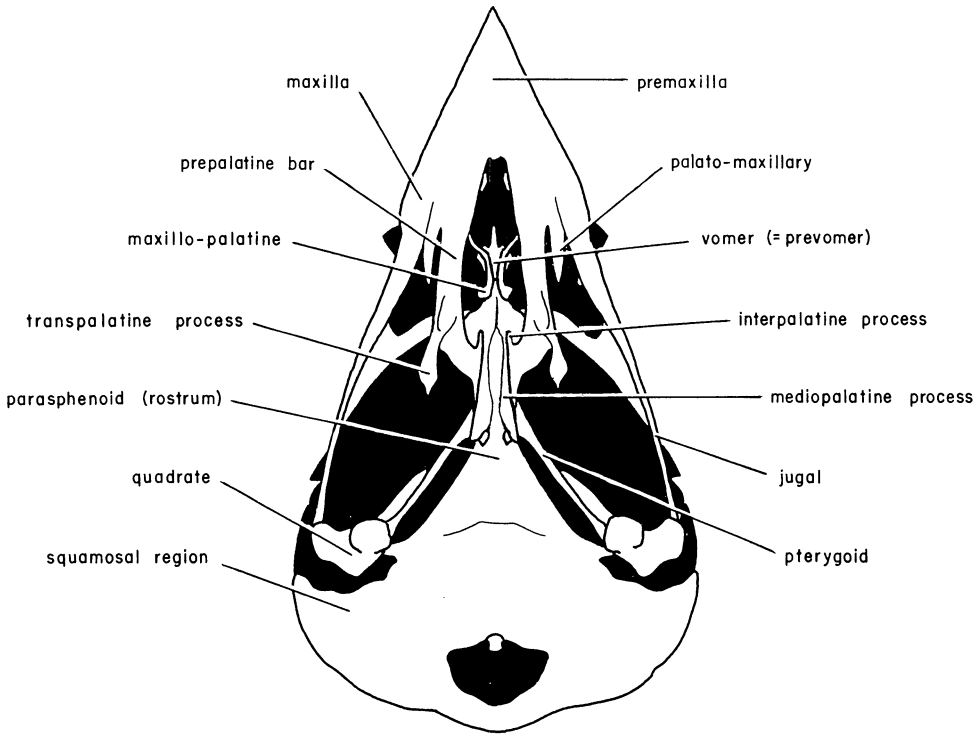
- Marshall, William H.
1940 More Notes on Salt-feeding of Red Crossbills. *Condor*, 42:218-19.
- Matthew, William Diller
1939 *Climate and Evolution*. N. Y. Acad. Sci., Special Publ., 1:i-xii + 1-223.
- Mayr, Ernst
1946 *History of the North American Bird Fauna*. *Wilson Bull.*, 58:3-41.
- Mayr, Ernst, and Dean Amadon
1951 *A Classification of Recent Birds*. *Amer. Mus. Novitates*, No. 1496.
- Parker, W. K.
1878 On the Skull of the Aegithognathous Birds, Part II. *Trans. Zool. Soc. London*, 10:251-314.
- Peterson, James G.
1942 Salt Feeding Habits of the House Finch. *Condor*, 44:73.
- Ridgway, Robert
1901 *The Birds of North and Middle America*. *Bull. U. S. Natl. Mus.*, 50, Pt. 1.
- Roberts, Thomas S.
1936 *The Birds of Minnesota*. Vol. 2. Minneapolis: Univ. Minn. Press.
- Setzer, Henry W.
1949 Subspeciation in the Kangaroo Rat, *Dipodomys ordii*. *Univ. Kans. Publ., Mus. Nat. Hist.*, 1:473-573.
- Shufeldt, R. W.
1888 The Osteology of *Habia melanocephala*, with Comparative Notes upon the Skeletons of Certain Other Conirostral Birds and of Tanagers. *Auk*, 5:438-44.
1890 *The Myology of the Raven (Corvus corax sinuatus)*. New York: Macmillan and Co.
- Stegmann, B.
1938 Principes généraux des subdivisions ornithogéographiques de la région paléarctique. *Faune de l'URSS (N.S. 19)*, L'Oiseaux, 1, No. 2.
- Sushkin, Peter P.
1924 [On the Fringillidae and Allied Groups.] *Bull. Brit. Ornith. Club*, 45:36-39.
1925 The Evening Grosbeak (*Hesperiphona*), the Only American Genus of a Palaeartic Group. *Auk*, 42:256-61.
1927 On the Anatomy and Classification of the Weaver-birds. *Bull. Amer. Mus. Nat. Hist.*, 57:1-32.
1929 On the Systematic Position of the *Drepanidae*. *Verhandl. VI Internatl. Ornith. Kongr. Kopenhagen, 1926*, pp. 379-81.
- Weaver, Richard Lee, and Franklin H. West
1943 Notes on the Breeding of the Pine Siskin. *Auk*, 60:492-504.
- Wetmore, Alexander
1940 *A Systematic Classification for the Birds of the World*. *Smithson. Misc. Coll.*, 99, No. 7:1-11.
- Witherby, H. F., F. C. R. Jourdain, Norman F. Ticehurst, and Bernard W. Tucker
1938 *The Handbook of British Birds*. Vol. 1. London: H. F. and G. Witherby.
- Wolters, Hans E.
1949 Die Finkenvögel (I). *Beitr. z. Gattungssyst. d. Vögel*, 1:3-17.

EXPLANATION OF FIGURES

The drawings of skulls, in palatal view, of finches and allied birds are diagrammatic. They are intended to show in detail only the relationships of the bones of the palate to each other and to other bones approximately in the palatal plane. Skull structures dorsal to the palatal plane are represented as if in a single background plane.

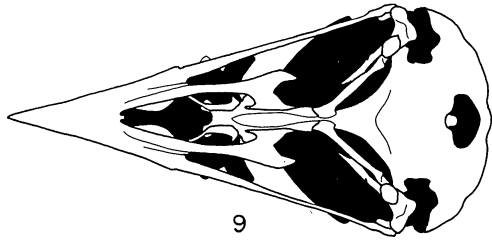
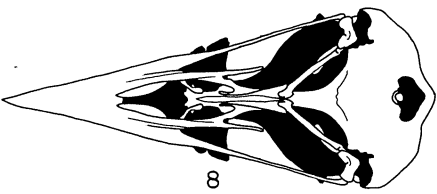
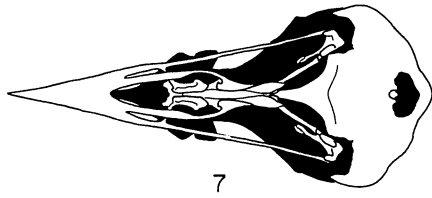
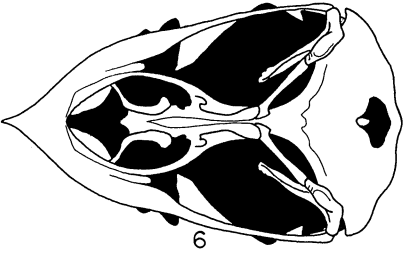
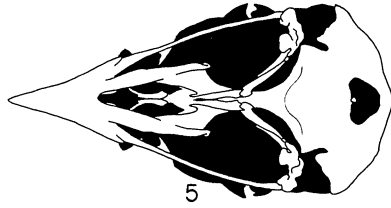
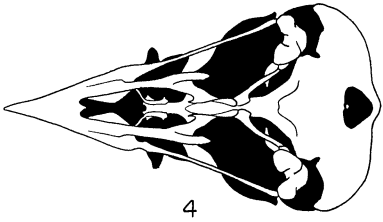
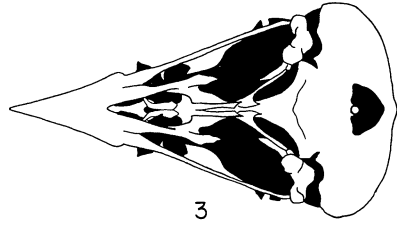
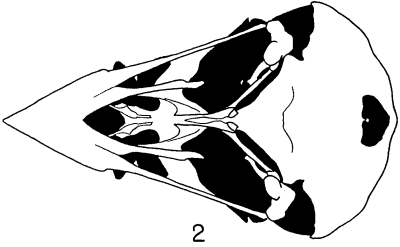
The abbreviations preceding the catalogue numbers of the specimens figured are as follows: UMMZ — University of Michigan Museum of Zoology; MVZ — University of California Museum of Vertebrate Zoology; KU — University of Kansas Museum of Natural History; USNM — United States National Museum; AMNH — American Museum of Natural History; GMS — collection of George M. Sutton; HBT — collection of Harrison B. Tordoff.

Fig. 1. *Spiza americana*, ♂, UMMZ 72848, with important bones labeled. This drawing, with its labels, will serve as a key to identification of various bones on the following, unlabeled drawings.

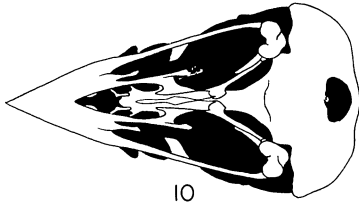


1.

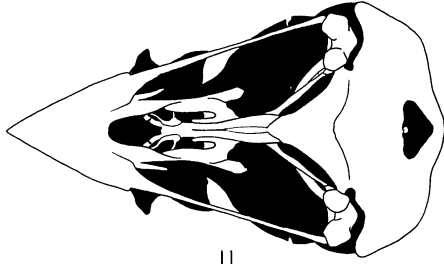
- Fig. 2. *Dolichonyx oryzivorus*, ♀, HBT 632.
Fig. 3. *Agelaius phoeniceus*, ♀, HBT 608.
Fig. 4. *Icterus galbula*, ♀, HBT 582.
Fig. 5. *Molothrus ater*, ♂, HBT 563.
Fig. 6. *Tersina viridis*, ♂, AMNH 2511.
Fig. 7. *Diglossa baritula* (transpalatine processes broken off), ♂, UMMZ 119293.
Fig. 8. *Chlorophanes spiza*, ♂, UMMZ 119299.
Fig. 9. *Icteria virens*, ♂, KU 14429.



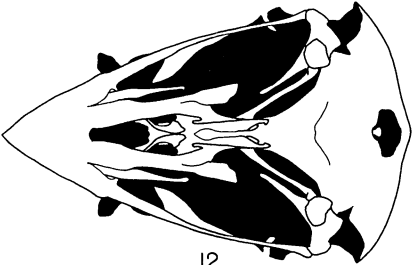
- Fig. 10. *Passerina cyanea*, ♂, HBT 630.
Fig. 11. *Cyanocopsa parellina*, ♀, GMS 10935.
Fig. 12. *Guiraca caerulea*, ♂, HBT 744.
Fig. 13. *Pheucticus ludovicianus*, ♂, HBT 622.
Fig. 14. *Pyrrhuloxia sinuata*, ♂, GMS 10490.
Fig. 15. *Richmondia cardinalis*, ♂, HBT 479.
Fig. 16. *Rhodothraupis celaeno*, ♀, GMS 10890.
Fig. 17. *Saltator atriceps*, ♂, GMS 10629.



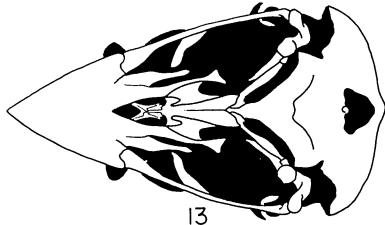
10



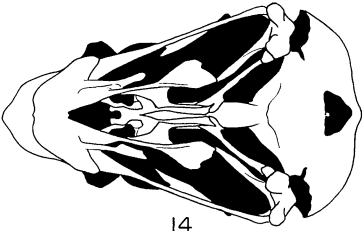
11



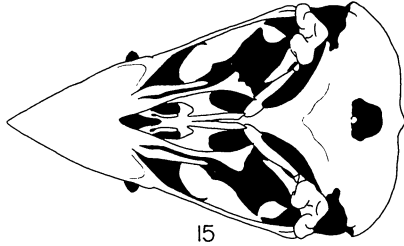
12



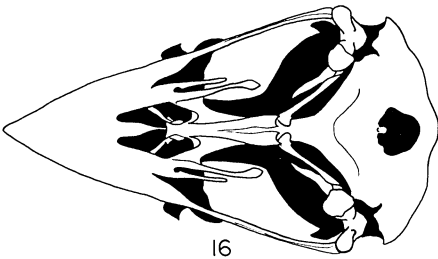
13



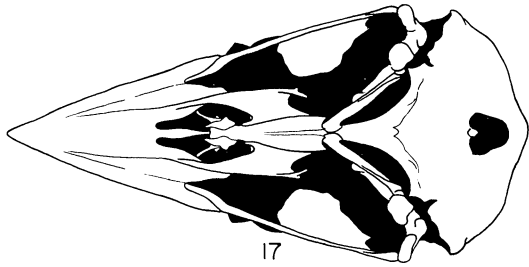
14



15

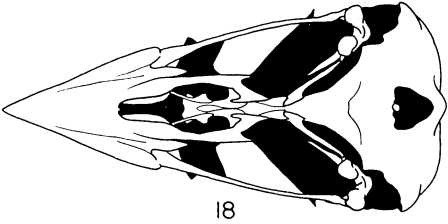


16

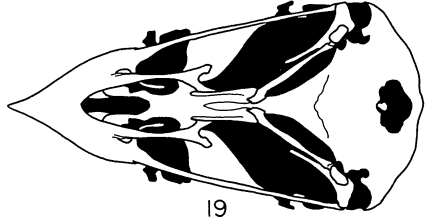


17

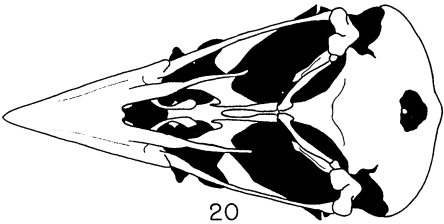
- Fig. 18. *Piranga flava*, ♀, GMS 10927.
Fig. 19. *Chlorophonia occipitalis*, ♀, UMMZ 119304.
Fig. 20. *Habia gutturalis*, ♂, GMS 10891.
Fig. 21. *Chlorospingus ophthalmicus*, ♂, KU 25020.
Fig. 22. *Melopyrrha nigra*, ♀, HBT 774.
Fig. 23. *Tiaris canora*, ♂, HBT 601.
Fig. 24. *Geospiza magnirostris*, ♂, MVZ 93082.
Fig. 25. *Pinaroloxias inornata*, ♂, USNM 318775.



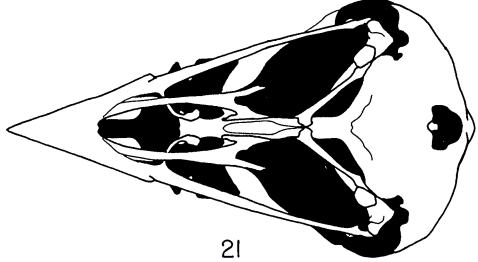
18



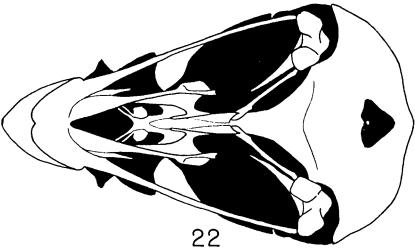
19



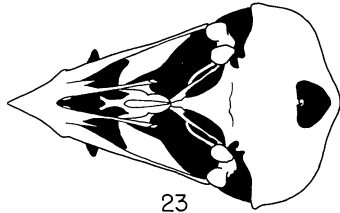
20



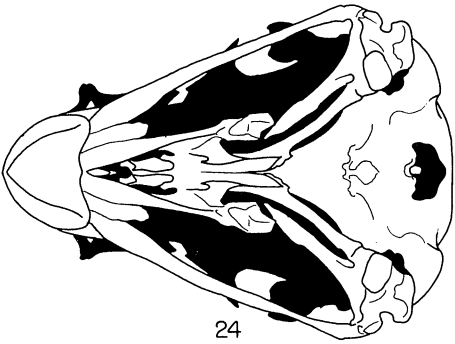
21



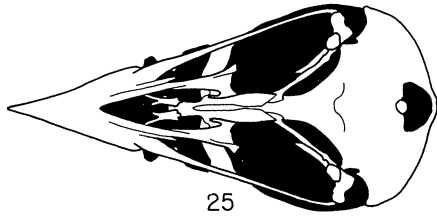
22



23

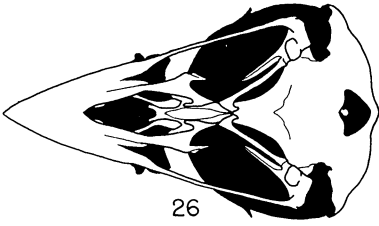


24

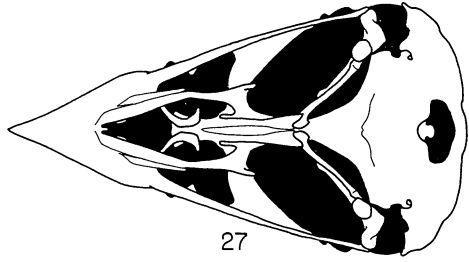


25

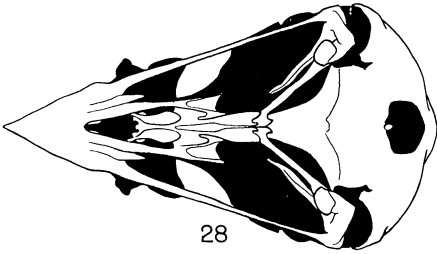
- Fig. 26. *Fringilla coelebs*, ♂, UMMZ 119094.
Fig. 27. *Melophus lathami*, ♂, USNM 322038.
Fig. 28. *Emberiza calandra*, ♀, UMMZ 119289.
Fig. 29. *Plectrophenax nivalis*, ♂, HBT 504.
Fig. 30. *Calcarius lapponicus*, ♂, HBT 557.
Fig. 31. *Saltatricula multicolor*, ♀, USNM 227436.
Fig. 32. *Embernagra platensis*, ♂, USNM 227429.
Fig. 33. *Poospiza melanoleuca*, ♂, USNM 227442.



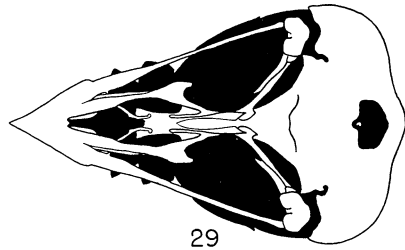
26



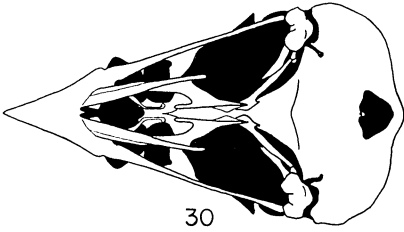
27



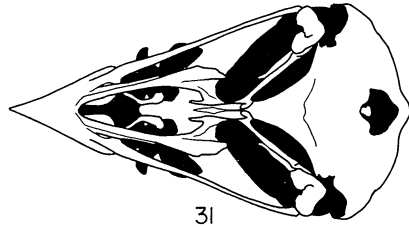
28



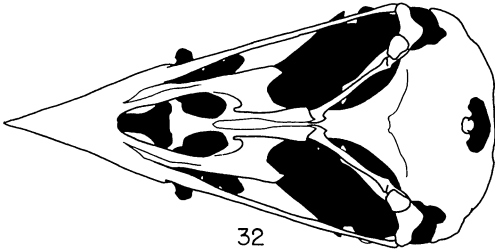
29



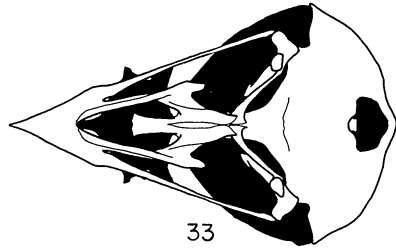
30



31

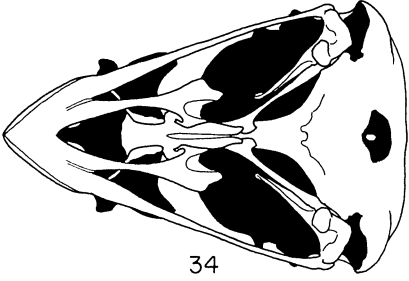


32

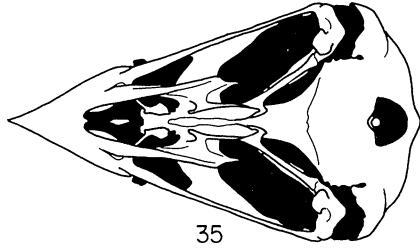


33

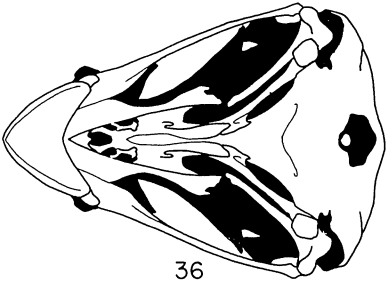
- Fig. 34. *Gubernatrix cristata*, ♂, USNM 227540.
Fig. 35. *Paroaria coronata*, sex ?, UMMZ 119256.
Fig. 36. *Loxigilla violacea*, ♂, UMMZ 118156.
Fig. 37. *Sporophila torqueola*, ♀, GMS 10485.
Fig. 38. *Oryzoborus angolensis*, ♀, USNM 346154.
Fig. 39. *Atlapetes brunnei-nucha*, ♂, GMS 10882.
Fig. 40. *Atlapetes torquata*, sex ?, GMS 10922.
Fig. 41. *Arremonops rufivirgatus*, ♀, GMS 10548.



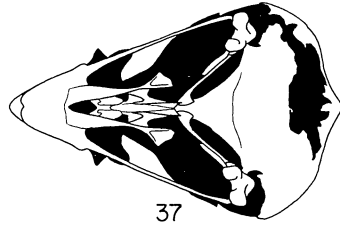
34



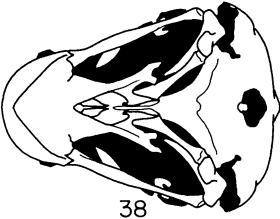
35



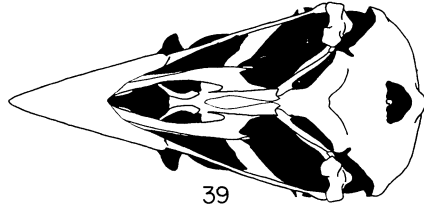
36



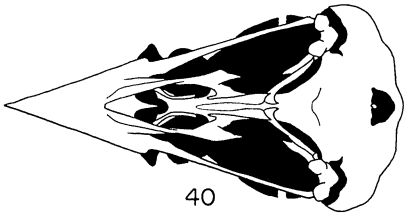
37



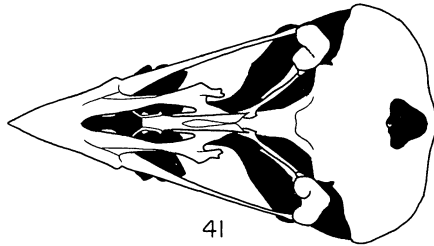
38



39

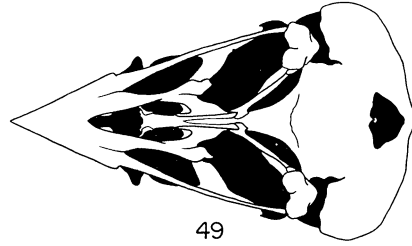
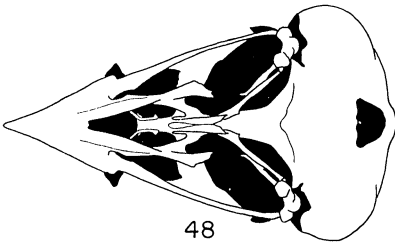
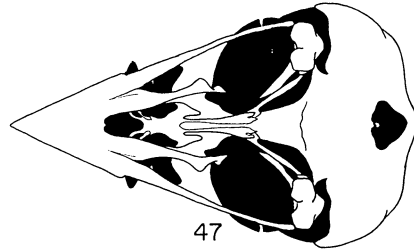
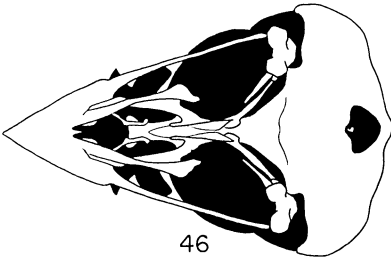
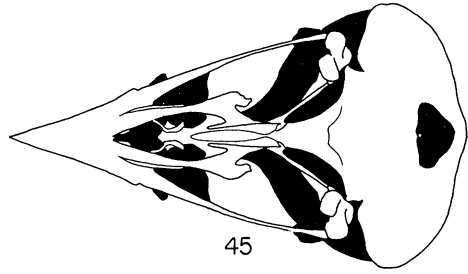
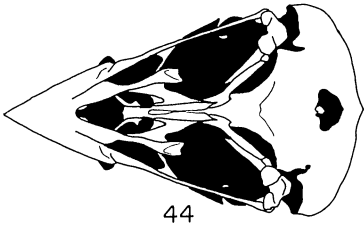
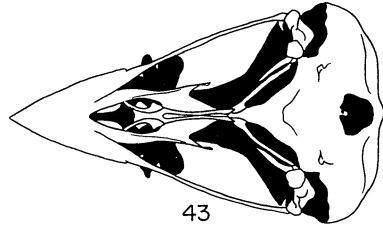
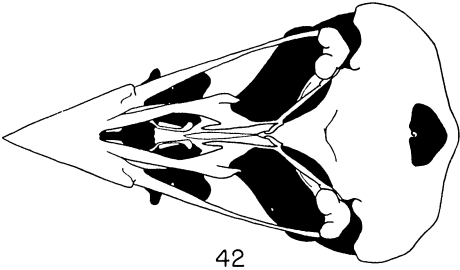


40

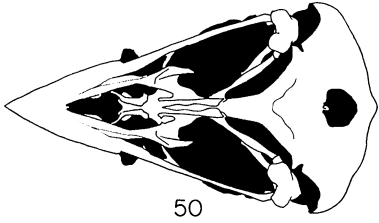


41

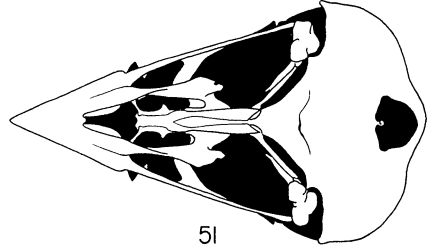
- Fig. 42. *Chlorura chlorura*, ♀, GMS 10510.
Fig. 43. *Pipilo erythrophthalmus*, ♀, HBT 627.
Fig. 44. *Calamospiza melanocorys*, ♂, GMS 10458.
Fig. 45. *Passerculus sandwichensis*, ♂, HBT 569.
Fig. 46. *Ammodramus savaamarum*, ♂, HBT 573.
Fig. 47. *Passerherbulus henslowii*, ♂, HBT 575.
Fig. 48. *Poocetes gramineus*, ♀, HBT 612.
Fig. 49. *Chondestes grammacus*, ♀, HBT 610.



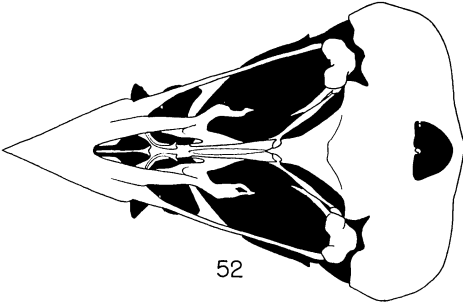
- Fig. 50. *Aimophila rufescens*, ♂, HBT 640.
Fig. 51. *Amphispiza bilineata*, ♂, GMS 10468.
Fig. 52. *Junco phaeonotus*, ♂, GMS 10924.
Fig. 53. *Spizella pusilla*, ♂, HBT 585.
Fig. 54. *Spizella pusilla*, ♀, HBT 629.
Fig. 55. *Zonotrichia leucophrys*, ♂, HBT 604.
Fig. 56. *Passerella iliaca*, ♂, HBT 548.
Fig. 57. *Melospiza melodia*, ♂, HBT 534.



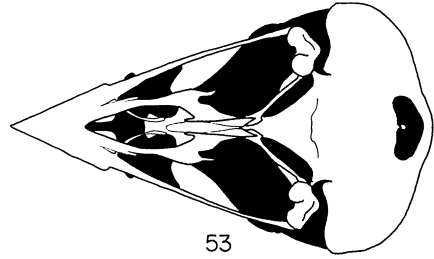
50



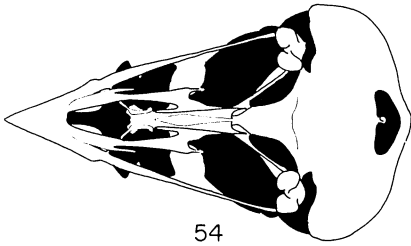
51



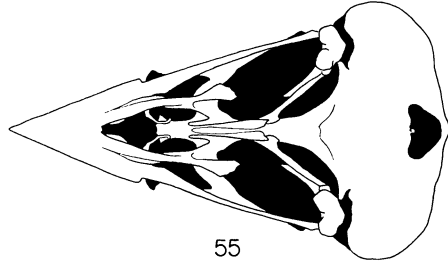
52



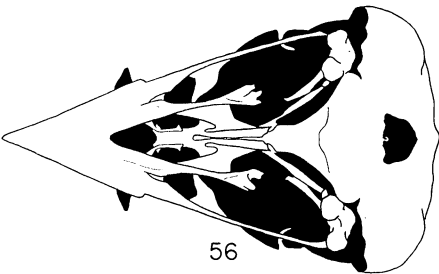
53



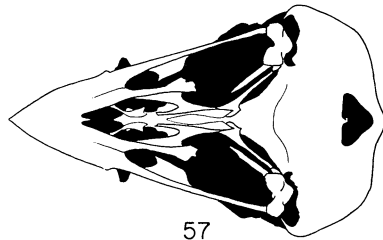
54



55

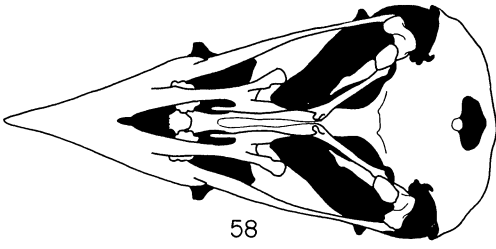


56

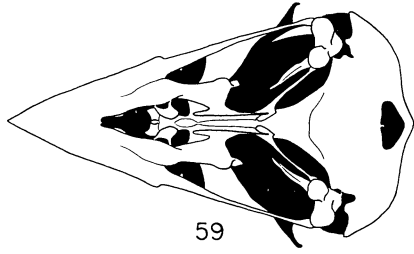


57

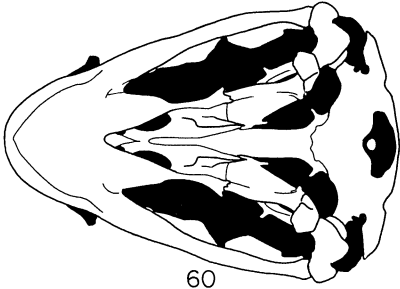
- Fig. 58. *Bubalornis albirostris*, sex ?, AMNH 2614.
Fig. 59. *Passer domesticus*, ♂, HBT 638.
Fig. 60. *Amblyospiza albifrons*, ♂, USNM 322508.
Fig. 61. *Ploceus cucullatus*, ♂, AMNH 2811.
Fig. 62. *Diatropura procne*, ♂, USNM 345659.
Fig. 63. *Quelea sanguirostris*, ♂, USNM 322307.
Fig. 64. *Steganura paradisea*, ♂, USNM 347602.
Fig. 65. *Erythrura psittacea*, ♂, USNM 346738.



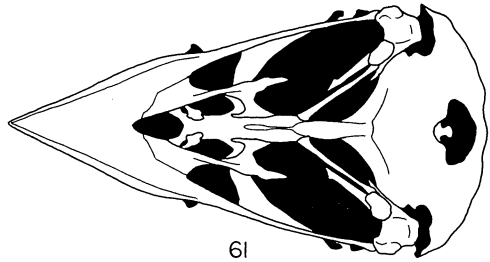
58



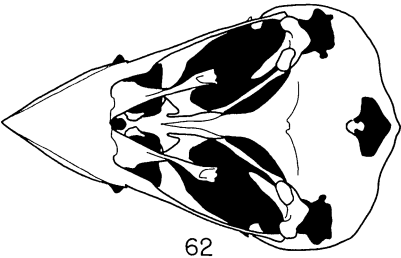
59



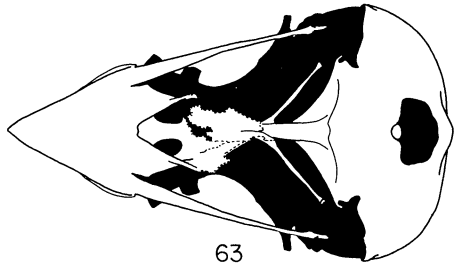
60



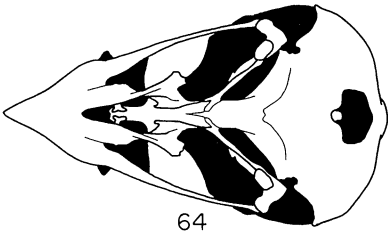
61



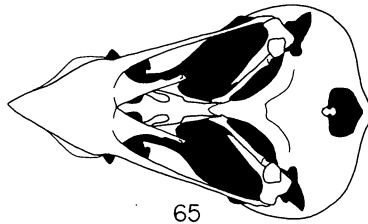
62



63



64



65

- Fig. 66. *Amadina fasciata*, ♀, USNM 427953.
Fig. 67. *Poephila gouldiae*, sex ?, USNM 346184.
Fig. 68. *Mycerobas melanoxanthus*, ♀, USNM 292174.
Fig. 69. *Hesperiphona vespertina*, ♂, HBT 500.
Fig. 70. *Chloris chloris*, ♀, UMMZ 119074.
Fig. 71. *Carpodacus purpureus*, ♀, HBT 522.
Fig. 72. *Pinicola enucleator*, ♀, UMMZ 74247.
Fig. 73. *Leucosticte tephrocotis*, ♂, HBT 494.

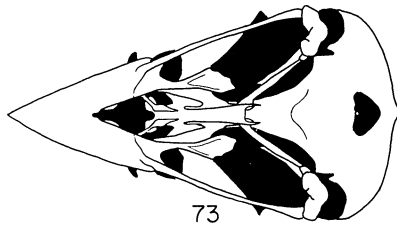
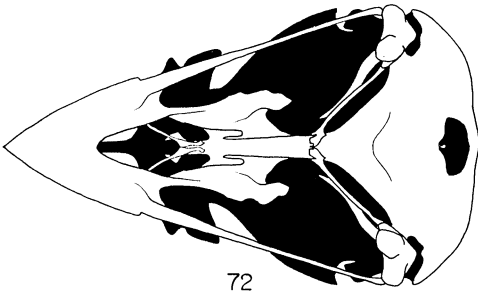
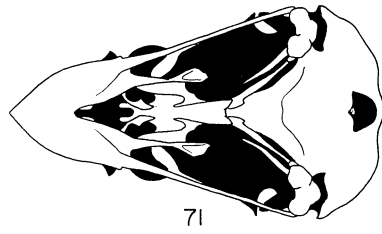
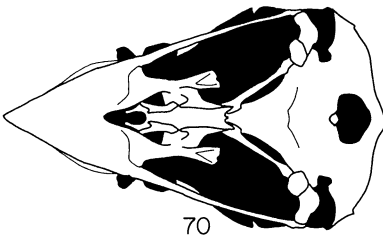
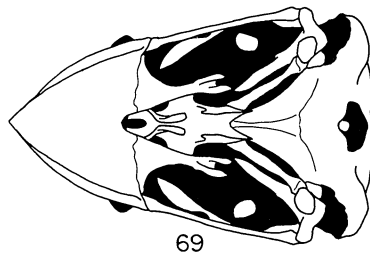
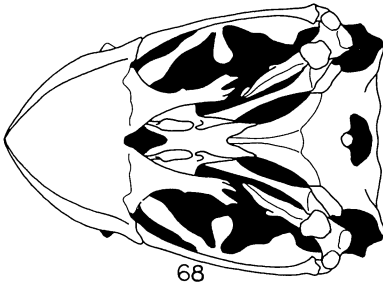
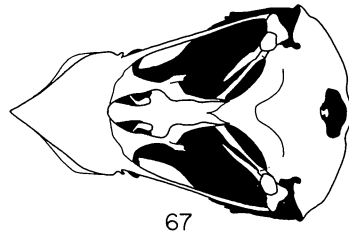
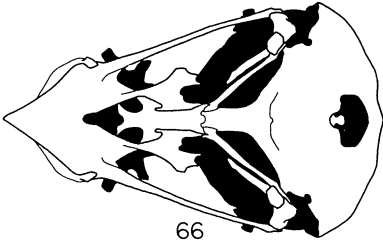
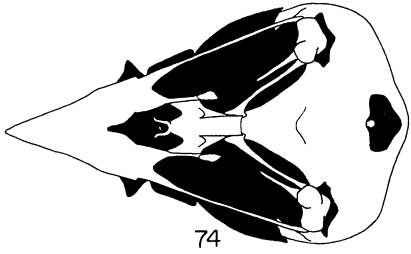


Fig. 74. *Carduelis carduelis*, ♀?, UMMZ 72847.

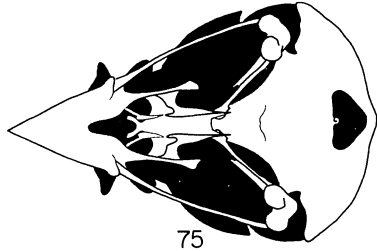
Fig. 75. *Acanthis flammea*, ♂, HBT 508.

Fig. 76. *Spinus psaltria*, ♂, GMS 10932.

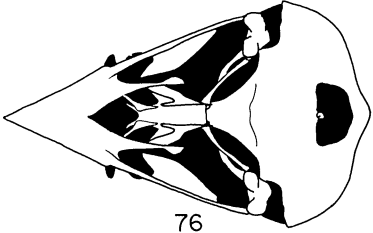
Fig. 77. *Loxia curvirostra*, sex ?, HBT 724.



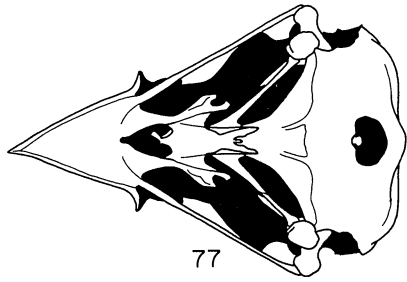
74



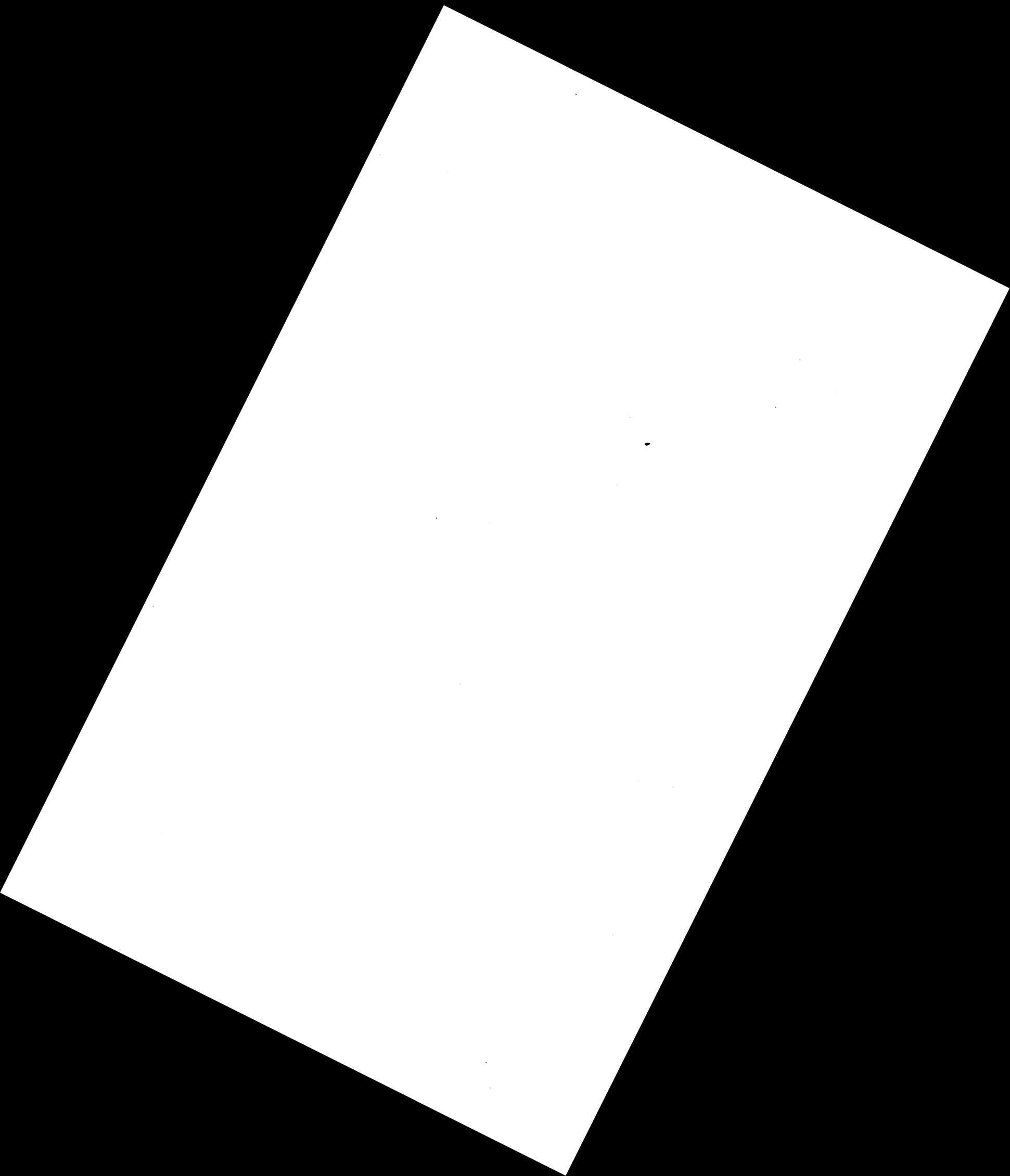
75

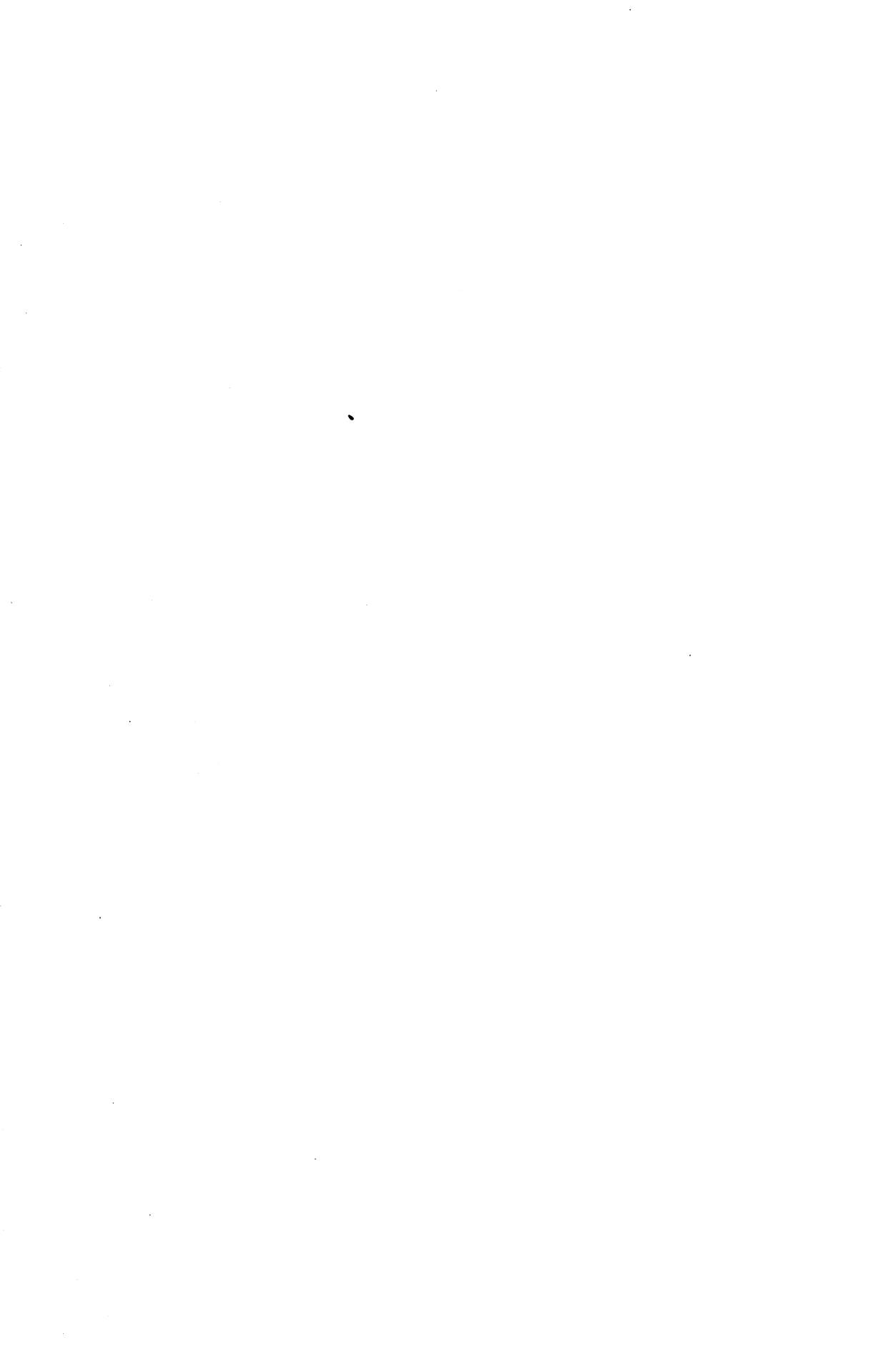


76



77





No. 30. The Darters of the Genera <i>Hololepis</i> and <i>Villora</i> . By Carl L. Hubbs and Mott Dwight Cannon. (1935) Pp. 93, 3 plates, 1 figure	\$0.50
No. 31. Goniobasis of the Coosa River, Alabama. By Calvin Goodrich. (1936) Pp. 60, 1 plate, 1 figure	\$0.35
No. 32. Following Fox Trails. By Adolph Murie. (1936) Pp. 45, 6 plates, 6 figures	\$1.00
No. 33. The Discovery of the Nest of the Colima Warbler (<i>Vermivora crissalis</i>). By Josselyn Van Tyne. (1936) Pp. 11, colored frontis., 3 plates, 1 map	\$0.35
No. 34. Mollusca of Petén and North Alta Vera Paz, Guatemala. By Calvin Goodrich and Henry van der Schalie. (1937) Pp. 50, 1 plate, 1 figure, 1 map	\$0.50
No. 35. A Revision of the Lamprey Genus <i>Ichthyomyzon</i> . By Carl L. Hubbs and Milton B. Trautman. (1937) Pp. 109, 2 plates, 5 figures, 1 map	\$2.00
No. 36. A Review of the Dragonflies of the Genera <i>Neurocordulia</i> and <i>Platycordulia</i> . By Francis Byers. (1937) Pp. 36, 8 plates, 4 maps	\$0.50
No. 37. The Birds of Brewster County, Texas. By Josselyn Van Tyne and George Miksch Sutton. (1937) Pp. 119, colored frontis., 5 plates, 1 map	\$1.25
No. 38. Revision of <i>Sciurus variegatoides</i> , a Species of Central American Squirrel. By William P. Harris, Jr. (1937) Pp. 39, 3 plates (2 colored), 3 figures, 1 map	\$0.50
No. 39. Faunal Relationships and Geographic Distribution of Mammals in Sonora, Mexico. By William H. Burt. (1938) Pp. 77, 26 maps.	\$0.75
No. 40. The Naiad Fauna of the Huron River, in Southeastern Michigan. By Henry van der Schalie. (1938) Pp. 83, 12 plates, 28 figures, 18 maps	\$1.00
No. 41. The Life History of Henslow's Sparrow, <i>Passerherbulus henslowi</i> (Audubon). By A. Sidney Hyde. (1939) Pp. 72, 4 plates, 3 figures, 1 map.	\$0.75
No. 42. Studies of the Fishes of the Order Cyprinodontes. XVI. A Revision of the Goodeidae. By Carl L. Hubbs and C. L. Turner. (1939) Pp. 85, 5 plates.	\$0.90
No. 43. Aquatic Mollusks of the Upper Peninsula of Michigan. By Calvin Goodrich and Henry van der Schalie. (1939) Pp. 45, 2 maps.	\$0.50
No. 44. The Birds of Buckeye Lake, Ohio. By Milton B. Trautman. (1940) Pp. 466, 15 plates and a frontis., 2 maps	\$2.50
No. 45. Territorial Behavior and Populations of Some Small Mammals in Southern Michigan. By William H. Burt. (1940) Pp. 58, 2 plates, 8 figures, 2 maps.	\$0.50
No. 46. A Contribution to the Ecology and Faunal Relationships of the Mammals of the Davis Mountain Region, Southwestern Texas. By W. Frank Blair. (1940) Pp. 39, 3 plates, 1 map	\$0.35
No. 47. A Contribution to the Herpetology of the Isthmus of Tehuantepec. IV. By Norman Hartweg and James A. Oliver. (1940) Pp. 31	\$0.35
No. 48. A Revision of the Black Basses (<i>Micropterus</i> and <i>Huro</i>) with Descriptions of Four New Forms. By Carl L. Hubbs and Reeve M. Bailey. (1940) Pp. 51, 6 plates, 1 figure, 2 maps	\$0.75
No. 49. Studies of Neotropical Colubrinae. VIII. A Revision of the Genus <i>Dryadophis</i> Stuart, 1939. By L. C. Stuart. (1941) Pp. 106, 4 plates, 13 figures, 4 maps.	\$1.15
No. 50. A Contribution to the Knowledge of Variation in <i>Opheodrys vernalis</i> (Harlan), with the Description of a New Subspecies. By Arnold B. Grobman. (1941) Pp. 38, 2 figures, 1 map	\$0.35
No. 51. Mammals of the Lava Fields and Adjoining Areas in Valencia County, New Mexico. By Emmet T. Hooper. (1941) Pp. 47, 3 plates, 1 map	\$0.50
No. 52. Type Localities of Pocket Gophers of the Genus <i>Thomomys</i> . By Emmet T. Hooper. (1941) Pp. 26, 1 map	\$0.25
No. 53. The Crane Flies (<i>Tipulidae</i>) of the George Reserve, Michigan. By J. Speed Rogers. (1942) Pp. 128, 8 plates, 1 map	\$1.25
No. 54. The Ecology of the Orthoptera and Dermaptera of the George Reserve, Michigan. By Irving J. Cantrall. (1943) Pp. 182, 10 plates, 2 maps	\$1.50
No. 55. Birds of the Gulf Lowlands of Southern Mexico. By Pierce Brodtkorb. (1943) Pp. 88, 1 map	\$0.75
No. 56. Taxonomic and Geographic Comments on Guatemalan Salamanders of the Genus <i>Oedipus</i> . By L. C. Stuart. (1943) Pp. 33, 2 plates, 1 map	\$0.35
No. 57. The Amnicolidae of Michigan: Distribution, Ecology, and Taxonomy. By Elmer G. Berry. (1943) Pp. 68, 9 plates, 10 figures, 10 maps	\$0.85
No. 58. A Systematic Review of the Neotropical Water Rats of the Genus <i>Nectomys</i> (<i>Cricetinae</i>). By Philip Hershkovitz. (1944) Pp. 88, 4 plates, 5 figures, 2 maps	\$1.15
No. 59. San Francisco Bay as a Factor Influencing Speciation in Rodents. By Emmet T. Hooper. (1944) Pp. 89, 5 plates, 18 maps	\$1.25
No. 60. The Fresh-Water Triclad of Michigan. By Roman Kenk. (1944) Pp. 44, 7 plates, 5 figures	\$0.50
No. 61. Home Range, Homing Behavior, and Migration in Turtles. By Fred R. Cagle. (1944) Pp. 34, 2 plates, 4 figures, 1 map	\$0.35
No. 62. Monograph of the Family Mordellidae (Coleoptera) of North America, North of Mexico. By Emil Liljeblad. (1945) Pp. 229, 7 plates	\$2.00

No. 63. Phylogenetic Position of the Citharidae, a Family of Flatfishes. By Carl L. Hubbs. (1945) Pp. 38, 1 figure	\$0.35
No. 64. <i>Goniobasis livescens</i> of Michigan. By Calvin Goodrich. (1945) Pp. 36, 1 plate, 1 figure, 1 map	\$0.35
No. 65. Endemic Fish Fauna of Lake Waccamaw, North Carolina. By Carl L. Hubbs and Edward C. Raney. (1946) Pp. 30, 1 plate, 2 maps	\$0.35
No. 66. Revision of <i>Ceraticthys</i> , a Genus of American Cyprinid Fishes. By Carl L. Hubbs and John D. Black. (1947) Pp. 56, 2 plates, 1 figure, 2 maps	\$1.00
No. 67. A Small Collection of Fishes from Rio Grande do Sul, Brazil. By A. Lourenço Gomes. (1947) Pp. 39, 3 plates, 2 figures	\$0.50
No. 68. The Cyprinodont Fishes of the Death Valley System of Eastern California and Southwestern Nevada. By Robert R. Miller. (1948) Pp. 155, 15 plates, 5 figures, 3 maps	\$2.00
No. 69. The Amphibians and Reptiles of Alta Verapaz, Guatemala. By L. C. Stuart. (1948) Pp. 109, 10 figures, 1 map	\$1.50
No. 70. The Land and Fresh-water Mollusks of Puerto Rico. By Henry van der Schalie. (1948) Pp. 134, 15 plates, 4 figures, 64 maps	\$2.50
No. 71. The Animal Life of Temporary and Permanent Ponds in Southern Michigan. By Roman Kenk. (1949) Pp. 66, 3 plates, 7 figures, 1 map	\$1.00
No. 72. Faunal Relationships of Recent North American Rodents. By Emmet T. Hooper. (1949) Pp. 28	\$0.35
No. 73. A Study of Small Mammal Populations in Northern Michigan. By Richard H. Manville. (1949) Pp. 83, 4 plates, 6 figures, 1 map	\$1.25
No. 74. Studies of the Nesting Birds of the Edwin S. George Reserve. Part I. The Vireos. By George M. Sutton. (1949) Pp. 37, 5 plates	\$1.00
No. 75. The Birds of Michigan. By Norman A. Wood. (1951) Pp. 559, 16 plates, 1 map.	\$4.00
No. 76. Studies of the Black Swamp Snake, <i>Seminatrix pygaea</i> (Cope), with Descriptions of Two New Subspecies. By Herndon G. Dowling. (1950) Pp. 38, 6 figures, 1 map	\$1.25
No. 77. A Systematic Review of the Harvest Mice (Genus <i>Reithrodontomys</i>) of Latin America. By Emmet T. Hooper. (1952) Pp. 255, 9 plates, 24 figures, 12 maps	\$4.00
Cloth bound	\$4.60
No. 78. Studies of Cyprinodont Fishes. XX. A New Subfamily from Guatemala, with <i>Ctenoid</i> Scales and a Unilateral Pectoral Clasper. By Carl L. Hubbs. (1950) Pp. 28, 4 plates, 1 map	\$1.25
No. 79. An Analysis of Some Physical Factors Affecting the Local Distribution of the Short-tail Shrew (<i>Blarina brevicauda</i>) in the Northern Part of the Lower Peninsula of Michigan. By William O. Pruitt, Jr. (1953) Pp. 39, 9 figures	\$0.60
No. 80. A Comparative Study of the Osteology and Myology of the Cranial and Cervical Regions of the Shrew, <i>Blarina brevicauda</i> , and the Mole, <i>Scalopus aquaticus</i> . By George R. L. Gaughran. (1954) Pp. 82, 67 figures	\$1.00
No. 81. A Systematic Study of the Avian Family Fringillidae, Based on the Structure of the Skull. By Harrison B. Tordoff. (1954) Pp. 42, 77 Figures	\$0.75
No. 82. The Meibomian Glands of Voles and Lemmings (Microtinae). By Wilbur B. Quay. (1954) Pp. 24, 3 plates, 3 figures	\$0.15
No. 83. The Comparative Myology of the Mammalian Genera <i>Sigmodon</i> , <i>Oryzomys</i> , <i>Neotoma</i> , and <i>Peromyscus</i> (Cricetinae), With Remarks on Their Intergeneric Relationships. By George C. Rinker. (In press).	
No. 84. The Burrowing Beetles of the Genus <i>Mycotrupes</i> (Coleoptera: Scarabaeidae: Geotrupinae). By Ada L. Olson, T. H. Hubbell, and H. F. Howden. (1954) Pp. 59, 8 plates, 3 figures	\$0.75