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CONTRIBUTIONS IN SCIENCE

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

PAPERS IN AVIAN PALEONTOLOGY HONORING HILDEGARDE HOWARD

edited by Kenneth E. Campbell, Jr.

Published by the NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY • 900 EXPOSITION BOULEVARD • LOS ANGELES, CALIFORNIA 90007

SERIAL PUBLICATIONS
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The scientific publications of the Natural History Museum of Los Angeles County have been issued at irregular intervals in three major series; the articles in each series are numbered individually, and numbers run consecutively, regardless of subject matter:

- Contributions in Science, a series of miscellaneous technical papers describing original research in the life and earth sciences.
- Science Bulletins, a series of miscellaneous monographs describing original research in the life and earth sciences. This series was discontinued in 1978 with the issue of Numbers 29 and 30; monographs are now published by the Museum in the Contributions in Science series.
- Science Series, long articles on natural history topics, generally written for the layman.

Copies of the publications in these series are available on an exchange basis to institutions and individual researchers. Copies are also sold through the Museum Bookshop.

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ABSTRACT: Nineteen papers in avian paleontology—including theoretical aspects, faunal studies, reviews of specific groups, the description of several new forms, and archaeological studies—are presented here to honor Hildegarde Howard. Preceding these are appreciations by Theodore Downs, Jean Delacour, and Herbert Friedmann; a review of the contributions of Hildegarde Howard by Kenneth E. Campbell, Jr.; the bibliography of Hildegarde Howard; an index to avian taxa described by Hildegarde Howard; and the illustrations of avian osteology from "The Avifauna of Emeryville Shellmound" by Hildegarde Howard. George G. Simpson reviews the development of the field of paleornithology, discusses the evolution of birds, and reviews the evolution of penguins. Joel Cracraft reviews the principles of cladistic analysis and discusses their application to studies in avian paleontology. Cécile Mourer-Chauviré reviews the archaeotrogonids of the Eocene and Oligocene Phosphorites du Quercy, France, erecting a separate family for the group and describing the fourth known species of *Archaeotrogon*. Ella Hoch reviews the middle Eocene oilshale deposits of Messel, West Germany, and describes a new genus and species of shorebird with columboid features from that site. Storrs L. Olson rediagnoses the family Plotopteridae Howard, describes a new genus and species of plotopterid from late Oligocene deposits of Washington, and discusses plotopterid adaptations. Kenneth E. Campbell, Jr., and Eduardo P. Tonni review the family Teratornithidae L. Miller, describe a new genus and species of teratorn from the Huayquerian (late Miocene) of Argentina, and briefly review teratorn cranial adaptations. E.N. Kurochkin describes new species of *Palaeoaramides, Rallus,* and *Crex* from middle Pliocene deposits of Western Mongolia, and comments on what these fossil rails indicate as to the paleoclimate and paleoecology of that region. Larry D. Martin and Robert M. Mengel describe a new species of *Anser* from the late Pliocene (Blancan) Broadwater Local Fauna of western Nebraska, and reconstruct the body proportions of the new goose by comparing the size of its limb bones to those of Recent geese. Pierce Brodkorb describes a new species of *Ardea* from the Plio/Pleistocene deposits of Shungura, Ethiopia, and changes the systematic position of four fossil species previously assigned to the Ardeidae. Pat Vickers Rich reviews the family Dromornithidae, extinct large ratites known from Miocene to late Pleistocene deposits of Australia, and comments on relationships between the various groups of ratites. Eduardo P. Tonni reviews the present state of knowledge of Cenozoic birds of Argentina and presents preliminary data on new finds. Alan Feduccia describes a new species of *Burhinus* from Pleistocene (Sangamon) deposits of Kansas and discusses the paleoecological and paleoclimatic implications of the presence of this tropical genus in North America during the Pleistocene. Kenneth E. Campbell, Jr., reviews the Rancholabrean avifauna of the Itchtucknee River, Florida, and notes the presence of the tropical genus *Milvago* in Florida. David W. Steadman reviews the osteology and paleontology of all known species of living and fossil turkeys, concluding that the Meleagridinae is comprised of three genera, *Rhegminornis* Wetmore, *Proagriocharis* Martin and Tate, and *Meleagris* Linnaeus; that all diagnostic specimens of Blancan and younger ages, including both living species, are referable to *Meleagris*; and that *M. gallopavo* has been present in southeastern United States since at least the Blancan. Amadeo M. Rea analyzes turkey remains from 17 southwestern late Quaternary sites; concludes that all pre-agricultural turkeys are referable to *Meleagris crassipes*; and proposes that *M. gallopavo* was imported into the southwest by paleoindians and became a feral population, *M. g. merriami,* with the breakdown of southwestern cultures. Charmion R. McKusick analyzes remains of three different forms of turkeys from southwestern archaeological sites, and discusses how the three forms may have developed. Paul Parmalee analyzes the avian remains from Archaic and Fremont sites of Utah, and discusses how birds may have been utilized by the prehistoric inhabitants of Utah. Pat Vickers Rich and A.R. McEvey describe a fossil Plain Wanderer (Pedionomidae), and use the specimen to date the Morwell Fire-hole deposits of southeastern Victoria, Australia. Lyndon L. Hargrave and Steven D. Emslie discuss the first Holocene records of the Passenger Pigeon, *Ectopistes migratorius,* from New Mexico.

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PREFACE

In July 1980, Hildegarde Howard entered her fifty-second year with the Natural History Museum of Los Angeles County. She began her career by spending many of her student years working with the Museum's collections, and went on to become one of the Museum's best known and most respected scientists. Her interests in the Museum and her chosen field, avian paleontology, have never diminished, and her continuing research is an inspiration to us all. To honor her past achievements and to show our appreciation for her continuing contributions to avian paleontology, we present this festschrift.

The editor is especially indebted to Joanne Baker who dealt so effectively with the preparation of the manuscripts and the voluminous correspondence related to the festschrift. He also expresses his appreciation to the contributors who have worked so hard to make this festschrift possible, and thanks Lidia Lustig and Antonia Tejada-Flores for translation of foreign language manuscripts. The frontispiece is by Lawrence Reynolds, Museum Photographer, who also provided copies of the earlier photographs of Dr. Howard. The editor gratefully acknowledges the assistance of the following people who formed the review committee for this publication:

William A. Akersten
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APPRECIATIONS

HILDEGARDE HOWARD

Hildegarde Howard first became involved in the activities of the Natural History Museum of Los Angeles County in 1921, just 11 years after the ground-breaking ceremony for the original Museum structure. Her very distinguished career in avian paleontology began in 1924 when she initiated her studies of the fossil birds from Rancho La Brea under the careful tutelage of Loye Miller. Her enthusiasm for and participation in the field of avian paleobiology is undiminished to this day.

Dr. Howard was born 3 April 1901 in Washington, D.C., and in 1906 moved to Los Angeles with her parents. Her father was a writer, often composing and editing scripts for the movie studios in Hollywood; her mother was a musician and composer. Dr. Howard published the first of her 140 papers on avian paleontology, general science, curation, and other matters in an international high school natural history bulletin in 1923. In 1924, she began working at the Museum with the title of "Day Laborer." She met her husband, Henry Anson Wylde (who became Chief of Exhibits at the Museum), during that year, when they were both assigned to sorting La Brea fossils in the basement of the original Museum building.

From 1924 to 1928, Dr. Howard received her B.A., M.A., and Ph.D. degrees at the University of California, Berkeley. Dr. Howard worked as an assistant in Zoology at the University of California, Los Angeles, and as a research associate at the Los Angeles County Museum during the same period. In Berkeley and in Los Angeles, she was greatly influenced by association and study with Loye Miller, Pirie Davidson (later Mrs. Maverick), Chester Stock, William Diller Matthew, Joseph Grinnell, and William H. Burt (to name a few). Loye Miller was especially inspirational to her in her scientific and philosophical outlook. Dr. Howard assumed her first official permanent position with the Museum, entitled Junior Clerk, in February 1929, although she actually began working full-time in the Museum in 1928. Despite the titles, she was in reality a curator, perhaps the first true specialist in avian paleontology.

Dr. Howard has been the most productive curator-scientist associated with this museum. It is fortunate for avian paleontology that she has resided for so long in the Los Angeles area, thus being readily available to identify and study the fossil birds constantly being uncovered in the environment of erosion and man's development in the southern California marine coastal sediments.

Throughout her career, Dr. Howard (along with the late Chester Stock) championed the scientific, educational, and historical aspects of the Rancho La Brea site in Hancock Park. Unlikely as it may seem, defenses had to be constantly implemented to preserve the site in the proper manner. As a result of Dr. Howard's efforts, the birds from Rancho La Brea were by far the best curated fossil vertebrates in the Museum's collection.

During her tenure as Chief Curator of Science in the 1950's, Dr. Howard was largely responsible for the important increase in the professional staff of the Museum. I have always been impressed by her ability to effectively set aside time for concentration on research in spite of the days in her career that demanded administrative function or service to the public.

After retirement in 1961, Dr. Howard became a Guggenheim Fellow, completing the research for her paper entitled "Fossil Birds from the Anza-Borrego Desert," an important southwest avifauna of the early to mid-Pleistocene, and carrying on research on other fossil birds of the western United States. Her research on Rancho La Brea birds continues: for example, in 1974 she described new elements of the relatively rare La Brea Condor, *Breagyps clarki.* We count on her working one day per week at the Museum as Chief Curator Emeritus, and she has a complete study at her home in Laguna Hills, California.

Dr. Howard has long been a member of the American Association for the Advancement of Science (fellow); Society of Vertebrate Paleontology (Honorary Life Member); California and Southern California Academies of Sciences (fellow); American Ornithologists' Union (fellow); Cooper Ornithological Society (Honorary Life Member); Geological Society of America (fellow); Phi Sigma; Phi Beta Kappa; and Sigma Xi. For her outstanding contribution to avian paleontology, she was awarded the distinguished Brewster Memorial Award in 1953 by the American Ornithologists' Union. She is an honorary member of the Soroptimists Club of Miracle Mile near Rancho La Brea, a member of the Church of the Brethren, and she is active in a diversity of group programs in the community in which she lives. She is also proud to be a Research Associate of the Santa Barbara Museum of Natural History.

In 1973, the California Academy of Sciences honored Dr. Howard as a distinguished California Scientist and featured a special public exhibit of her works. This not only substantiated our pride in Dr. Howard but fulfilled a rarely recognized need for joining the layman and scientist in an effective yet simple way. The Hildegarde Howard Cenozoic Hall in the Natural History Museum of Los Angeles County was opened in 1977 and honors her as this museum's most eminent paleontologist. The imaginative new exhibits at the George C. Page Museum of La Brea Discoveries, which appropriately highlight the diversity of the La Brea avifauna, also boldly accentuate the results of Dr. Howard's scientific work.

Dr. Howard is relatively little known as a private person, except to a few close colleagues and friends. She is not a devotee of meetings or conferences and seems to treasure privacy and select friends or associates (part of this relates to a long-standing hearing problem). However, when asked, she always presents a clearly stated view of her opinion or observation and rarely spends time in argumentative ramblings. She has a good feeling for the problems of a museum and the people in the trenches—for many years she was there. There are some people whose presence seems to add respectability to any situation or organization; this is certainly true of Hildegarde Howard.

My original introduction to fossils was a master's thesis study of a late Pleistocene avifauna from Kansas in 1947–1948. I benefited from the counsel of Hildegarde Howard in that study, as I have many times since. Perhaps this early study unconsciously influenced her decision to hire me for my first job as Curator of Vertebrate Paleontology at the Museum in 1952, even though I had already wandered "astray" into the field of paleomammalogy. I consider it a privilege to be a part of this recognition of the outstanding contributions made by Hildegarde Howard to the science of avian paleontology and to the growth and stature of all the sciences at the Natural History Museum of Los Angeles County during the past 50 years. Reviewing the papers in this volume has rekindled my appreciation of our "unfeathered friends" and the investigators of their fragile remains. And it reminds me of how Hildegarde has often declared, when in less serious mood, that she preferred to see the birds without the feathers when identifying a specimen.

It was in 1976 that papers were published to honor another eminent scholar, the late Dr. Alexander Wetmore. Again, in 1980, we have published records herein that further support Dr. Storrs Olson's comment in the Wetmore volume that "avian paleontology is truly experiencing a renaissance." We are very grateful for Dr. Howard's contribution to the foundation of the renaissance and for her continued participation.

THEODORE DOWNS
Chief Curator Emeritus
Earth Science Division
Natural History Museum of
Los Angeles County

A TRIBUTE TO DR. HILDEGARDE HOWARD

My memory of Dr. Hildegarde Howard is a long one. I first met her in 1936, when she was a young assistant curator at the Natural History Museum of Los Angeles County. I was spending the winters in Pasadena, in the company of the late Masauji Hachisukse, a Japanese ornithologist educated in France and in England, and, at that time, we met many of our colleagues in southern California. Most of the younger generation had been trained by Loye Miller, a prominent professor at the University of California, Los Angeles, who was their patriarchal mentor. They called him "Padre," and Hildegarde was one of his preferred students. Her interests in ornithology are specialized: she is a paleontologist, one of the world authorities on fossil birds. I can only say that my appreciation of her knowledge is such that I asked her, some 25 years ago, to contribute a special chapter on all known fossil anatids for my four volume work, "The Waterfowl of the World."

I want, however, to state particularly here my appreciation of Dr. Howard's achievements as Chief Curator of Science (Natural History) at the Natural History Museum of Los Angeles County, a position she held during the 9 years of my directorship of that institution (1952–1960). Science in those days was one of the four divisions of the Museum, the others being History, Art, and Education. I had to attend to all of them. Although I am a biologist, I could only devote a part of my time to the Science Division. I therefore relied upon Dr. Howard for its management. I sincerely believe that no one could have done it better—her experience, her authority, and her understanding of people and problems were perfect. During all those years, we worked together in complete harmony, and I trust that our combined efforts resulted in a definite improvement of the collections and of their presentations to the public, as well as in a better standing of our Museum in the scientific world.

Dr. Howard retired 1 year after I, having reached the mandatory retirement age, had myself left the Museum. I cannot help feeling grateful that she was still there at the time of my departure. I would have missed her tremendously.

I am happy to pay here a tribute to a prominent scientist, to an outstanding administrator, and also to a very dear friend.

JEAN DELACOUR
Director Emeritus
Natural History Museum of
Los Angeles County

HILDEGARDE HOWARD AND THE MUSEUM: FIFTY YEARS

The prestige and scientific importance of a great natural history museum are made by, and depend on, two main assets: the scope and quality of its research collections, and the expertise and devotion of its professional staff. Without these, no matter how extensive and excellent its exhibits and related programs may be, the museum would be purely a local educational institution and would never command a position of eminence in the learned world as a center of scholarship and as a treasure house of irreplaceable, original materials awaiting elucidation.

Seldom has the development of any major museum been so closely related to one individual member of its curatorial staff as has that of the Natural History Museum of Los Angeles County to the presence and the work of Dr. Hildegarde Howard. For half a century, from August 1929 to the present, she has been constantly concerned with the study of its ever growing collections of fossil birds. Indeed, for some of the early years of her association with the institution, she was practically the entire scientific staff of the museum, and later, as its programs and collections expanded and specialists in fields other than her own were added to the staff, she became the acknowledged head of the museum's scientific faculty. Although Dr. Howard officially retired in 1961, she has remained an active and productive contributor to the museum's research work, coming in to examine specimens at least once a week, and often taking them home for further study during the intervening days. In a very real sense the museum has been identified with her career, her scientific life, and although she has modestly kept from public acclaim, her colleagues on the museum staff and the knowledgeable members of its Board of Governors and of that of the Museum Alliance are well aware of how much the museum owes to her. The importance of her research on fossil birds is not only abundantly recognized by the enthusiastic response of the worldwide contributors to the present "Festschrift," but was signally acknowledged by the American Ornithologists' Union many years ago, in 1953, by their bestowal on her of their prized Brewster Medal. Also, shortly after her retirement from her position in the museum, the John Simon Guggenheim Memorial Foundation awarded her a fellowship with a travel and study stipend to enable her to continue and to extend her researches in paleornithology. As another testimonial to her work and influence, the museum officially named in her honor "The Hildegarde Howard Cenozoic Hall," an exhibition gallery devoted to a display of Cenozoic vertebrate fossils, the fauna of one of the geological periods to which she has devoted much study over many years.

It says much for Dr. Howard's ability to handle the many, and sometimes irksome, problems of people and events that inevitably arise in any sizeable institution that after her long association with the museum she is able to look back on 50 years remarkably free of personal animosities or institutional dilemmas. Her path was not always easy, but she knew how to make it not only smooth but steadily progressive. Her many friends and colleagues thank her for all she has done and extend their best wishes for a further continuation of this fine relationship.

HERBERT FRIEDMANN
Director Emeritus
Natural History Museum of
Los Angeles County

THE CONTRIBUTIONS OF HILDEGARDE HOWARD

By Kenneth E. Campbell, Jr.

Within the broad field of vertebrate paleontology, paleornithology was long considered to be a relatively minor subdiscipline. Few workers contributed to the field in a regular manner, and almost all of the early contributors worked with avian fossils as an aside to their main interests. Studies were conducted only when particularly interesting or complete specimens were found, or a notable collection of avian fossils was made from a single site. This rather haphazard growth in our knowledge of fossil birds continued well into the first half of this century. Slowly, however, there began a trend among a few workers to devote more and more of their efforts to the fledgling field of avian paleontology.

The earliest of the American workers who went on to become leaders in avian paleontology were the late Drs. Alexander Wetmore and Loye H. Miller. Their studies of fossil birds will continue as models of scientific integrity for generations to come. But these remarkable men were equally, if not more, prolific in their research and writing on modern birds. In 1976, a volume such as this present was dedicated to Dr. Wetmore in honor of his contributions to avian paleontology. That volume can be considered as marking the coming of age of paleornithology. But it is to Dr. Loye Miller that we owe a debt of gratitude for the first true specialist in avian paleontology: Dr. Hildegarde Howard.

Dr. Loye Miller began his work in fossil birds when the large collections of fossil vertebrates from the asphalt deposits at Rancho La Brea became available. The great quantity of bird fossils in these collections undoubtedly played an enormously influential role in the development of Dr. Miller's methods and approaches to the study of avian fossils, just as they were to play such an important role in Dr. Howard's career. By the time Dr. Miller became acquainted with a young student by the name of Hildegarde Howard, he had already published 16 papers on fossil birds from the Pacific states. Although most of these papers were concerned with the fossil birds from Rancho La Brea, he had barely scratched the surface of this large collection.

When Hildegarde Howard began attending the Southern Branch of the University of California (now known as University of California at Los Angeles, or UCLA) in 1920, she was not the least bit inclined toward a career in biology. Her first biology instructor, Miss Pirie Davidson, made the subject so interesting, however, that Dr. Howard not only became deeply interested in the subject but also began to work as a laboratory assistant in the class. At that time, Dr. Loye Miller was the chairman of the Biology Department. Through the efforts of Miss Davidson, Dr. Howard obtained a part-time job working for Dr. Chester Stock, a well-known mammalian paleontologist. Beginning in 1921, Dr. Howard worked for Dr. Stock sorting bones from Rancho La Brea in the basement of the Los Angeles Museum of History, Science and Art (now known as the Natural History Museum of Los Angeles County), even though he was at the time teaching at the University of California, Berkeley. In 1922, Dr. Howard went to Berkeley to finish her degree (UCLA was a two-year school at the time). At Berkeley, she took classes from Dr. Stock, while continuing to work for him.

When Dr. Howard completed her B.A. degree in 1924, Dr. Loye Miller offered her a position working part time at UCLA and part time at the Museum. During the school year 1924–25, her work for Dr. Miller at the Museum consisted primarily of research on the California Turkey from Rancho La Brea, *Meleagris* (=*Parapavo*) *californicus*. She obtained credit toward her Master's degree at Berkeley for this work, and it became the subject of her first major publication. It was this year that set Hildegarde Howard firmly toward her career in avian paleontology and a long period of collaboration with Loye Miller.

Dr. Howard returned to Berkeley in the fall of 1925 to continue her graduate work; she obtained her M.S. degree in 1926, her Ph.D. degree in 1928. Her dissertation, entitled "The Avifauna of Emeryville Shellmound," was not only a landmark achievement for her, but when published it became one of her most popular works. The work was a model of careful comparative research, and it has become a classic. One of the reasons for its impact was a series of drawings illustrating the bones of a bird skeleton, with clearly labeled osteological features (see p. xxvii, this vol.). For the first time avian paleontologists had a standard terminology, a clear point of reference for the works of different authors. This paper remains as the principle reference of its kind.

After returning to Berkeley in the fall of 1925, Dr. Howard continued to work at the Museum part time during breaks in her academic schedule. Upon receiving her Ph.D. degree she returned to Los Angeles where she began working fulltime at the Museum in 1928. She obtained a permanent position with the Museum in 1929: her title, Junior Clerk; her initial assignment, the curation of the fossils from Rancho La Brea and research on the birds of this collection. Hildegarde Howard's achievements in avian paleontology, including those that predate her formal association with the Museum, have made her one of the most recognized and respected scientists on the staff of this museum. Her works have contributed significantly to the status of this museum as a major research center, and for this we extend our deepest appreciation.

Over the span of her long career, Dr. Howard has published on a wide variety of problems in avian paleontology, but her papers can be grouped into general topics. While it is not possible to survey her many diverse achievements in detail, we can bring focus upon her major contributions. Throughout the remainder of this text, her papers are referred to by a number enclosed in parentheses; the numbers correspond to those found in her bibliography (see p. xvii, this vol.).

It was the tremendous collection of bird fossils from the asphalt deposits of Rancho La Brea, a collection numbering over 100,000 specimens, that formed Dr. Howard's training ground. Indeed, the names Hildegarde Howard and Rancho La Brea are readily recognized and connected by paleontologists of all

Hildegarde Howard at work on the birds of Rancho La Brea, 1939.

specialities the world over. It was this large collection that taught Dr. Howard the caution, restraint, and thoroughness in methodology that came to characterize her works. For, as many paleontologists have learned, it is far easier to describe a species when only one or two specimens are available than it is when hundreds of specimens are available. Few, however, have had the opportunity to learn this so early in their career as did Dr. Howard. She learned this lesson even before she began her graduate studies when she studied the fossil turkey from Rancho La Brea (2). Working with over 800 specimens representing all the major bones of the body, she discovered the critical importance of considering variability within a species before drawing any hard and fast conclusions. Considering the osteological variability found in turkeys (see the papers by Steadman, Rea, and McKusick herein), one can only speculate that perhaps Loye Miller had just this lesson in mind when he assigned her this group for her first research project.

Many of Dr. Howard's later works on the fossil birds from Rancho La Brea also involved studies of large numbers of specimens. For example, her studies of the eagles and eagle-like vultures of Rancho La Brea (12) involved the analysis of over *14,000* fossil specimens, and the study of the Rancho La Brea caracara (24) involved over 900 bones. These studies clearly reinforced the lessons of osteological variability that she had learned earlier.

Although much of Hildegarde Howard's career, and Loye Miller's as well, was devoted to the study of the fossil birds from Rancho La Brea, these collections are far from completely studied. While over 133 species have been reported from the site, major groups, such as the anatids, small raptors, and shorebirds, have yet to be analyzed in detail. This is not a result of a lack of continuing interest on Dr. Howard's part, but rather, of a lack of what she considered to be an adequate series of comparative material of extant species. The lack of sufficient series of skeletons of modern birds has always been the bane of paleornithologists, with the result that taxa are often described without due consideration for intraspecific variability. Although still true today, this problem was particularly acute during the early days of paleornithology. And when you have far more fossil specimens of a species than modern specimens, as did Dr. Howard, you learn to proceed with caution.

Dr. Howard's technical works on the fossil birds of Rancho La Brea fall into two categories: descriptive (2, 3, 5, 12, 14, 18, 22, 23, 24, 26, 38, 109, 137) and synthetic (7, 19, 96, 105). Her descriptive papers range from short notes (e.g., 3, 22) to monumental works encompassing more fossil specimens than any other paleornithologist has ever been privileged to study in a lifetime (e.g., 2, 12, 24). Characteristic of these papers, and all of her later descriptive papers, is the care with which she documents the assignment of a fossil to a species. Diagnostic osteological characters were always presented to justify the assignment of specimens to a species, along with an explanation as to why she considered the characters to be important. And, importantly, the explanations often carried references to the functional aspects of the features she discussed. If Dr. Howard felt any hesitancy in making her identifications, the reasons for this were clearly stated, thereby facilitating the labors of later workers.

The initial synthetic papers concerning Rancho La Brea presented analyses of the paleoavifauna as if it were representative of a single deposit, even though the collections from Rancho La Brea actually came from many different excavations, termed "pits." Many years after the early excavations ceased, it was discovered that the pits were not of the same age (96), nor were the compositions of the various pits necessarily similar (105). This discovery led to a program, now nearing completion, of radiocarbon dating of specimens from various levels of numerous pits. The completed series of dates will allow us to look for trends in avian evolution over the past 40,000 years. The fact that such trends exist and can be documented was first observed by Howard in her studies of the fossil birds from Rancho La Brea. This work led to the development of her concept of chronoclines, or temporal subspecies (see below). Howard's comparison of avian assemblages from the various pits of Rancho La Brea (105) has provided significant information pertaining to the paleoecology of the Los Angeles area and, by inference, much of southern California during the late Pleistocene. These studies have also provided information concerning the timing of late Pleistocene extinctions.

The second major focus of Dr. Howard's career has been the Tertiary marine birds of southern California. The explosive development of southern California as a major urban center, which began in earnest in the 1920's, has proven to be quite beneficial to paleornithology, although perhaps not to neornithology. The numerous new road cuts and excavations for industrial and housing developments have provided the paleontologists associated with the Natural History Museum of Los Angeles County and other institutions with the opportunity to collect fossils from deposits that would have other-

Hildegarde Howard in 1951.

Loye Miller presents Hildegarde Howard with the first fossil he collected at Rancho La Brea. The specimen, a vertebra of a sabertooth cat, was rescued from the spoilbank of J.C. Merriam's first excavation at Rancho La Brea in 1906, and presented to Dr. Howard in 1957.

wise remained inaccessible. Regrettably, most of the sites are covered shortly after exposure, thus limiting the size of the collections from any one site, but the ever-increasing rate of population growth in southern California is assurance that new sites will continue to be found. And, most fortunately, the increasing importance being attached to paleontological remains by local governmental institutions will ensure that more fossils will be collected in the future.

Most of the Tertiary deposits in southern California from which fossil birds have been collected are Miocene and Pliocene strata of marine origin. Consequently, all but a few of the Tertiary avian fossils found are seabirds. Most of the groups represented in collections from these deposits are common to the Pacific coast of North America today: e.g., loons, grebes, albatrosses, shearwaters, boobies, and auks. Fascinating extinct groups also formed an important part of the Tertiary avifauna of coastal California. These groups include the flightless auks of the subfamily Mancallinae, the "toothed" odontopterygiform birds of the genus *Osteodontornis,* and the flightless pelecaniform plotopterids. It is no exaggeration to state that Hildegarde Howard has led the way for our understanding of all of these groups, although she would be quick to point out that Loye Miller was also responsible for much of our knowledge of these seabirds.

It has indeed been fortunate for avian paleontology that Dr. Howard has been actively involved with the paleoavifaunas of the Pacific coast for such a long time. The continuity thus obtained has undoubtedly been of great assistance in developing her (and our) understanding of many of the fossil groups. For example, Dr. Howard's first published mention of the flightless diving auks of the genus *Mancalla* was in 1939 (27), her most recent work on members of the group was published in 1976 (138), and she is presently involved in new studies of these auks.

Through Dr. Howard's careful work, it is now possible to visualize the evolution of the flightless diving auks of the subfamily Mancallinae. The most primitive form known, described by Howard in 1966 (119), is the late Miocene *Praemancalla lagunensis.* This species shows distinct specialization toward flightlessness, but not to the degree found in the later species of *Mancalla.* A second species of *Praemancalla, P. wetmorei,* was described by Howard in 1976 (138). This late Miocene species was intermediate in characters between *P. lagunensis* and the early species of *Mancalla.*

Of the four known species of Pliocene *Mancalla,* Howard described two, *M. milleri* and *M. cedrosensis* (132), and Loye Miller described one, *M. diegense* (Miller 1937). The first known species of *Mancalla, M. californiensis* Lucas 1901, was the first fossil bird to be described from California. In 1968, Dr. Howard described a third genus of mancalline auk, *Alcodes* (123). The continual collection of new material of *Mancalla* has resulted in hundreds of specimens of this genus. As the collections grew, two reviews of the genus were published. The first was by Miller and Howard in 1949 (49), the second by Howard in 1970 (129). And, as mentioned above, Dr. Howard is presently hard at work on additional aspects of these auks. We look forward with great anticipation to her update on these interesting species of flightless birds.

But the mancalline auks were not the only species of flightless Tertiary marine birds revealed to us by Dr. Howard. Perhaps one of the most remarkable of Dr. Howard's achievements was her correct diagnosis of the group of flightless diving birds belonging to the family Plotopteridae from only the humeral end of a coracoid (126). Her diagnoses of plotopterid relationships and adaptations have been fully substantiated by recent discoveries of associated partial skeletons and single elements of at least three genera of plotopterids (see Olson, this vol.).

Many of the avian fossils from the Tertiary of the Pacific coast occur as skeletal impressions, or molds, on slabs of shale

Hildegarde Howard at the time of her retirement in 1961.

or diatomite. These specimens are difficult to work with because, although much of the skeleton may be represented by the impressions, it is not possible to obtain the fine details of structure necessary for description or comparison between specimens. Partial skeletons also occur, and although these provide more detailed structural information, the bones are only exposed on one side and they are quite often crushed. It was from just such a specimen as the latter type, and a most remarkable specimen at that, that Howard described the first odontopterygiform, or "toothed," bird from North America.

Osteodontornis orri was described by Howard (86) on the basis of an associated skeleton preserved on opposing surfaces of a shale slab. Although feather impressions were visible on the slab, osteological details were not well preserved. The unique "toothed" skull did, however, provide much information about the species and its relationships with other odontopterygiform species. Based on the lengths of the wing bones and feather impressions, Howard calculated the wingspread of *O. orri* to be upwards of 5–5½ meters, making it one of the largest flying birds known.

It was only a few years later that a second specimen of *Osteodontornis* was found. This specimen, which consisted of several skull fragments, was described by Howard and White (101) and referred to *O. orri*. In 1969, a third specimen of "toothed" bird was described by Howard, in conjunction with Stuart Warter (127). This specimen, from New Zealand, was also part of a skull, although of a different genus (*Pseudodontornis*); it provided additional information concerning the relationships of the odontopterygiform birds. We are indebted to Dr. Howard for her part in developing our understanding of these unique birds.

A number of Dr. Howard's papers on Tertiary marine birds (e.g., 8, 20, 48, 121, 123, 132, and 139) were faunal studies from particularly important fossil sites. Faunal studies are often difficult and time-consuming because of the variety of taxa involved and the small number of specimens of each taxon usually available from each site. Nevertheless, whenever a sufficient number of specimens accumulated from a site, or a site was only exposed for a short while before being lost, Dr. Howard felt it important that the available specimens be put on record. As a result of her persistent work with these small collections, we now have a basic, albeit limited, knowledge of the Tertiary avifaunas of the west coast, including information on many extinct species. For example, Dr. Howard described five extinct species of shearwaters in the papers listed above, along with new species of loons, albatrosses, sulids, and auks.

A distinctive feature of these works, as in all of Dr. Howard's studies, is the caution she used in describing new forms. If a specimen did not possess good, solid diagnostic characters, it was not given a name, even if she was convinced it represented a new form. Rather, such specimens were simply described, thus being put on record in the event similar, more diagnostic material should appear in the future. This approach has kept other workers abreast of new finds without cluttering the literature with names based on undiagnostic material.

Non-marine Tertiary avian fossils are normally relatively rare. An early exception to this rarity was a large collection of avian fossils from the Eocene of Patagonia, from which Dr. Howard described (80) a water bird of phoenicopterid character, now known as *Presbyornis antiquus* (Howard). Although recent work on *Presbyornis* by Alan Feduccia has resulted in the synonymy of the genus Howard erected for the species she described, her interpretations as to the nature of the species and its systematic relationships have been borne out.

Howard's contributions to our knowledge of other Tertiary birds include the description of the first Eocene birds known from California (116); the description of a Miocene hawk (35) and a Miocene thrush (87) from California; the description of a Miocene raptor and quail from South Dakota (120); and reports on Pliocene birds from Mexico (114, 118).

The major Pleistocene and prehistoric avifaunas that Dr. Howard described (excluding Rancho La Brea) came from several sources, including marine deposits, Pleistocene lake deposits, and cave deposits.

In western North America, many large lakes were formed and maintained by the climatic conditions that prevailed during periods of Pleistocene glacial activity. The lacustrine deposits that accumulated in these lakes have produced large collections of avian fossils. The most notable of these collections described by Dr. Howard are those from Fossil Lake, Oregon (39), and Manix Lake, California (83).

The paleoavifauna from Fossil Lake was particularly challenging because not only was it very large (over 2500 specimens identified to the family level, over 1800 of these to species), it was scattered through seven separate collections that had been made over a period of 60 years. Portions of this paleoavifauna had been described by E.D. Cope and R.W. Shufeldt in the late 1800's and early 1900's. The latter was not a particularly careful worker, and many of his species assignments were in error. Also, types were missing from the collections, or they had not been clearly identified in the original description of the species. Through her careful, meticulous work, Dr. Howard brought order to what had been a rather chaotic situation, and she placed the Fossil Lake avifauna in perspective with the other Pleistocene avifaunas known at the time.

It was in this paper that Dr. Howard first used the trinomial to designate chronoclinal variation. She knew that some late Pleistocene forms varied in predictable but relatively minor ways from their living counterparts and that overlap often existed between the fossil and living forms. In such cases, separation of the forms at the species level was considered unwise even though a difference clearly existed. Dr. Howard chose to make note of these differences by designating the fossil forms in question that had been previously named as new species as temporal subspecies. This represented a turnabout from an earlier opinion expressed by Dr. Howard that such subspecific relationships were "wholly untenable" (24:239). Although she had described a fossil subspecies in an earlier paper (28), she considered that case to be one of geographic, not temporal, variation (the second subspecies she named (122) was also an example of geographic variation). She discussed the chronocline concept in a later note (43), and it has played an important role in her analyses of late Pleistocene taxa (41).

In the discussion of the Fossil Lake avifauna, Dr. Howard described a number of specimens of a "pigmy goose" of the genus *Anabernicula,* but left the question as to their species assignment until she could give more time to the problem. In her later thorough review of the genus (112), she described the Oregon form as a new species and clarified the relationships of the genus within the Anseriformes.

Although the paleoavifauna of Manix Lake was small, it was important because it contained two species of flamingos. These were the first records of that group for California, although one of the species had been previously recorded from Fossil Lake, Oregon.

Another large collection described by Dr. Howard from Pleistocene deposits came from the Anza-Borrego Desert of southern California (107). She described several new species in this paper, and she also applied a technique for dating the paleoavifauna that she had used earlier in dating the various "pits" from Rancho La Brea (105). Based on relative numbers of extinct species, the technique cannot provide an exact age, but it can assist in correlating one paleoavifauna with another. For collections where absolute dating techniques are unavailable, this technique can prove to be useful in establishing relative ages.

The Pleistocene marine deposits, including those that occur on the Channel Islands off the coast of southern California, have proven to be important sources of avian fossils. Summaries of the avian fossils from these marine deposits were presented by Dr. Howard in 1949 (46) and 1958 (89). From these deposits have come large collections of the flightless diving geese of the genus *Chendytes.* In 1955 (82), Dr. Howard described the second known species of the genus *Chendytes, C. milleri,* from early Pleistocene deposits of San Nicolas Island. Interestingly, *C. milleri* was structurally more primitive, i.e., with less advanced wing reduction, than the late Pleistocene species, *C. lawi* L. Miller. Both before (42, 46) and after (111) her description of *C. milleri,* Howard described various limb elements of *Chendytes.* Recently, very large collections of *Chendytes* have become available, and they will undoubtedly tell us much more about the evolution of these flightless geese.

Cave deposits in New Mexico and Nevada provided large collections of avian fossils that were described by Dr. Howard (9, 13, 17, 66, 107, 131). The great majority of the specimens from these caves were assigned to living species, but there was also a consistent representation of extinct species. Thus, the cave deposits were considered to be of late Pleistocene, or possibly early Holocene, age. Dr. Howard pursued the description of these collections because she believed the fossil birds they contained would provide important distribution records for the species represented, living as well as extinct. The collections also contained an occasional new species, the most surprising of which was *Teratornis incredibilis* Howard (66). This species, to which Dr. Howard later referred two additional specimens (107, 135), was about 40% larger than *Teratornis merriami* Miller from Rancho La Brea, and about twice as large as the condor, *Gymnogyps californianus.* As she clearly stated, however, the relationships of this species cannot be accurately determined because no truly diagnostic element has been found.

On three occasions Dr. Howard published general reviews (21, 53, 140) of advances in avian paleontology, bringing non-paleornithologists up to date on progress in the field. She also undertook an even more extensive and difficult review of all fossil species of the order Anseriformes (110); several years later she updated this work (136). This review was not just a listing of all known fossil anseriform species. Rather, in the Howard tradition, all known osteological details of each fossil species were presented along with measurements and comments on possible relationships.

Hildegarde Howard also contributed numerous articles of a non-technical nature to the Museum's publications. These served to inform the public as to the Museum's activities and some of the intriguing fossils she and others were working on. In 1945, she published a general review of fossil birds with an emphasis on the birds of Rancho La Brea (37). This work was updated and expanded in 1955 (81) and 1962 (100). It remains a very popular publication with visitors to the Museum. Through these efforts, and her generous willingness to spend time with students and interested members of the general public, she engendered public support for the Museum.

Such a brief overview as this of a career as long and productive as that of Dr. Howard's can only hint at its depth and breadth. To survey Hildegarde Howard's contributions to paleornithology is to see a perfection of technique, the evolution of ideas, and devotion to a science. As the preeminent student of paleornithology, she has served her chosen field well. It is heartening and reassuring to know that her work continues.

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127. A new species of bony-toothed bird (Family Pseudodontornithidae) from the Tertiary of New Zealand. Rec. Canterbury Mus. 8(4):345–357, 4 pls. (With Stuart L. Warter) (May 31)
128. Avian fossils from three Pleistocene sites in central Mexico. Los Angeles Co. Mus., Contrib. Sci. 172:1–11, 1 text fig. (June 30)

1970

129. A review of the extinct avian genus, *Mancalla*. Los Angeles Co. Mus., Contrib. Sci. 203:1–12, 1 text fig. (November 24)

1971

130. In Memoriam: Loye Holmes Miller. Auk 88:276–285, photo. (April)
131. Quaternary avian remains from Dark Canyon Cave, New Mexico. Condor 73:237–240. (May 21)
132. Pliocene avian remains from Baja California. Los Angeles Co. Mus., Contrib. Sci. 217:1–17, 2 text figs. (November 12)

1972

133. Type specimens of avian fossils in the collections of the Natural History Museum of Los Angeles Co. Los Angeles Co. Mus., Contrib. Sci. 228:1–27. (June 7)
134. The bibliography of Loye Holmes Miller. Condor 74:268–271. (September)
135. The Incredible Teratorn again. Condor 74:341–344, 1 text fig. (September 18)

1973

136. Fossil Anseriformes. Pp. 233–326 (Chapter 10), and New General Corrections and Additions, pp. 371–378 (Chapter 12) *in* Waterfowl of the World by Jean Delacour. Second Edition. Vol. 4. Hamlyn Publ. Group, Ltd. (Country Life Ltd.), London.

1974

137. Postcranial elements of the extinct condor, ***Breagyps clarki*** (Miller). Los Angeles Co. Mus., Contrib. Sci. 256:1–24, 9 text figs. (May 22)

1976

138. A new species of flightless auk from the Miocene of California (Alcidae: Mancallinae). Smithsonian Contrib. to Paleobiology 27:141–146, 1 text fig. (May 21)

1978

139. Late Miocene marine birds from Orange Co., California. Los Angeles Co. Mus., Contrib. Sci. 290:1–28, 4 text figs. (March 21)

1979

140. Aves. Pp. 60–70 *in* The Encyclopedia of Paleontology (R.W. Fairbridge and D. Jablonski, Eds.). Dowden, Hutchinson, and Ross, Inc., Stroudsburg, Penn.

INDEX TO FOSSIL AVIAN TAXA DESCRIBED BY HILDEGARDE HOWARD

Listed below in alphabetical order are the fossil avian taxa described by Hildegarde Howard. Species are listed in the genera to which they were originally referred. Following each name is the publication number (from Dr. Howard's bibliography) and page in which the name was proposed.

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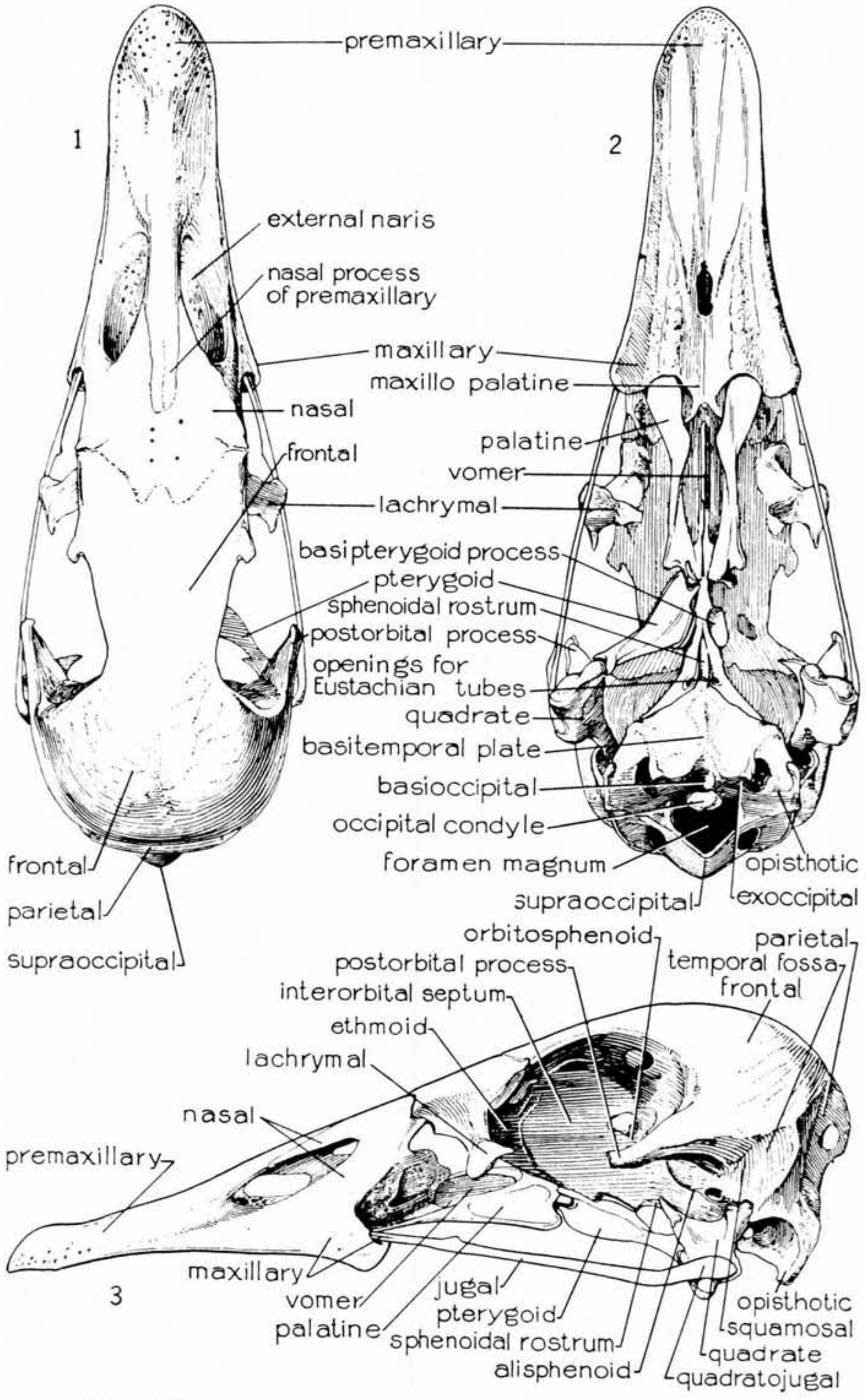
ILLUSTRATIONS OF AVIAN OSTEOLOGY TAKEN FROM "THE AVIFAUNA OF EMERYVILLE SHELLMOUND"

Of the many significant and invaluable contributions Hildegarde Howard has made to the field of avian paleontology, her paper entitled "The Avifauna of the Emeryville Shellmound" was one of the most important. This paper was published in 1929, and is especially cherished by those fortunate enough to obtain a copy. This work was not only a particularly valuable early contribution to avian paleontology, it contained a series of illustrations of the major bones of the avian skeleton with the major diagnostic features of each bone indicated and named. Over the past 50 years, these illustrations have proven very valuable, especially to new students of avian osteology. To this day they have not been surpassed for their usefulness as the terminology used in current studies of avian osteology remains based on that introduced by Dr. Howard. And anyone who has tried to orient a bone to determine view designations without the help of a mounted skeleton has often had cause to give thanks for the illustrations. That such a work remains so important after a period of 50 years testifies to its thoroughness and accuracy, two characters that have typified Dr. Howard's works through the years.

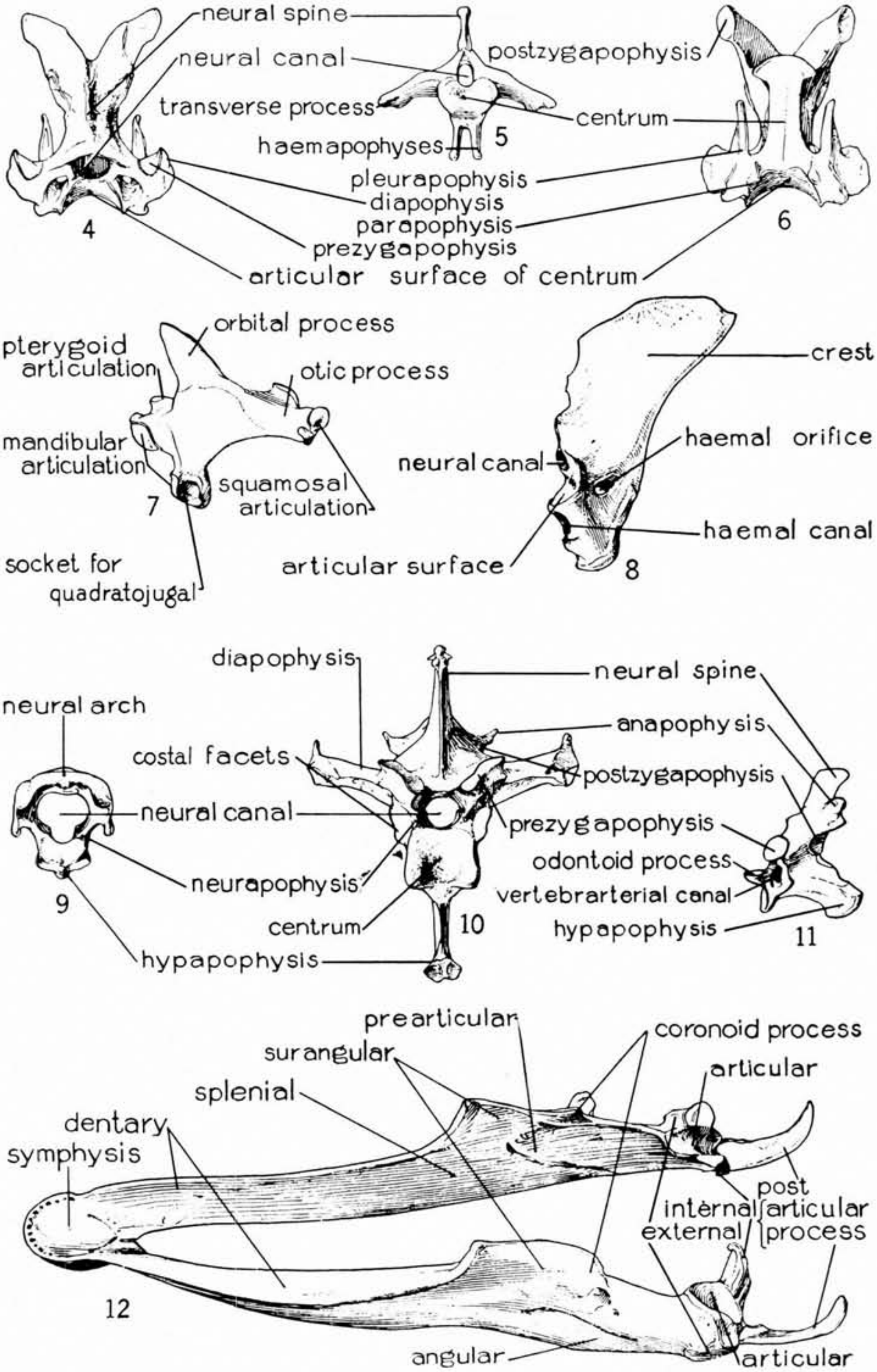
Even after 50 years Dr. Howard continues to receive many requests for copies of the Emeryville Shellmound paper; it is perhaps her most sought-after paper. For this reason we reproduce here the illustrations of avian osteological features from that paper. When speaking of the illustrations, Dr. Howard always credits William H. Burt for working with her in devising the nomenclatural system used in the illustrations, and Frieda Abernathy for executing the drawings. Quoted below are the explanatory notes for the illustrations, taken from page 325 of "The Avifauna of Emeryville Shellmound," by Hildegarde Howard, 1929, Univ. of California Publ. Zool. 32(2):301–394:

> Description of Species
>
> The terms employed in describing the diagnostic characters of the various represented species will be found in the accompanying series of labeled figures, drawn by Mrs. Frieda Abernathy.
>
> The system of nomenclature here set forth was devised by the writer in collaboration with Mr. William H. Burt, of the University of California. Papers by the following authorities were consulted: Furbringer (1888), Heilmann (1926), Lambrecht (1914), Lowe (1928), Miller (1925a, 1925b, 1927a), Milne-Edwards (1867–68), Owen (1866), Shufeldt (1890, 1909), Stresemann (1927), and Wetmore (1922, 1923). Dr. Miller and Dr. Wetmore were also consulted personally.
>
> The Golden Eagle (*Aquila chrysaetos*) and the Snow Goose (*Chen hyperboreus*) have been used for illustration. Such parts as cannot well be shown on *Aquila* are labeled on *Chen,* and vice versa. Of the Golden Eagle, Museum of Vertebrate Zoology specimen no. 28884 has been used except for figures 5 and 8, where MVZ no. 40866 was substituted; of the Snow Goose, MVZ no. 45555 has been drawn, except in figure 12 where MVZ no. 22446 has been used.

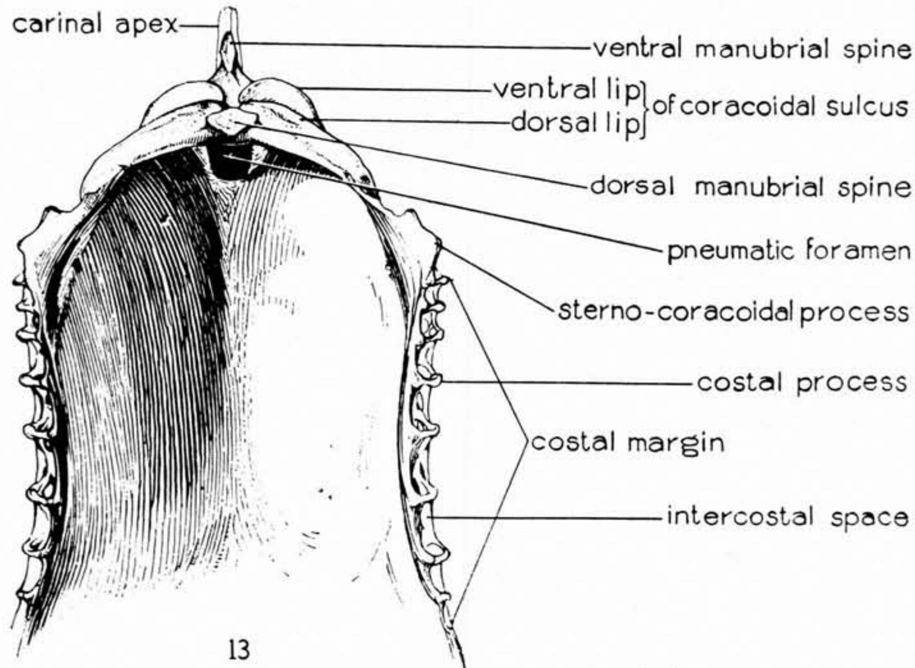
Grateful acknowledgment for permission to reprint the illustrations is given the University of California Press. Larry Reynolds provided unblemished photographs of the illustrations for reproduction here from a very well-worn copy of the original publication.



Skull of *Chen hyperboreus*. Fig. 1, dorsal view; fig. 2, ventral view; fig. 3, lateral view. × 1.



Figs. 4–11, *Aquila chrysaetos.* Fig. 4, 6th cervical vertebra, dorsal view; fig. 5, caudal vertebra, anterior view; fig. 6, 6th cervical vertebra, ventral view; fig. 7, left quadrate, external view; fig. 8, pygostyle; fig. 9, atlas, posterior view; fig. 10, 4th thoracic vertebra, anterior view; fig. 11, axis, left side; fig. 12, *Chen hyperboreus,* mandible. × 1.



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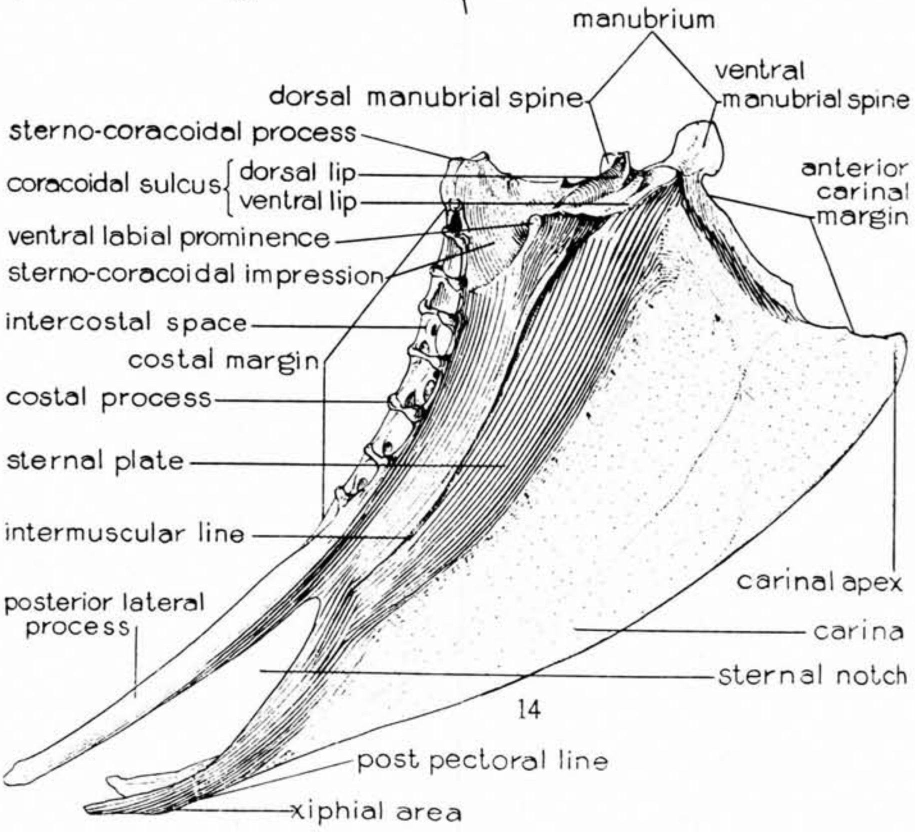

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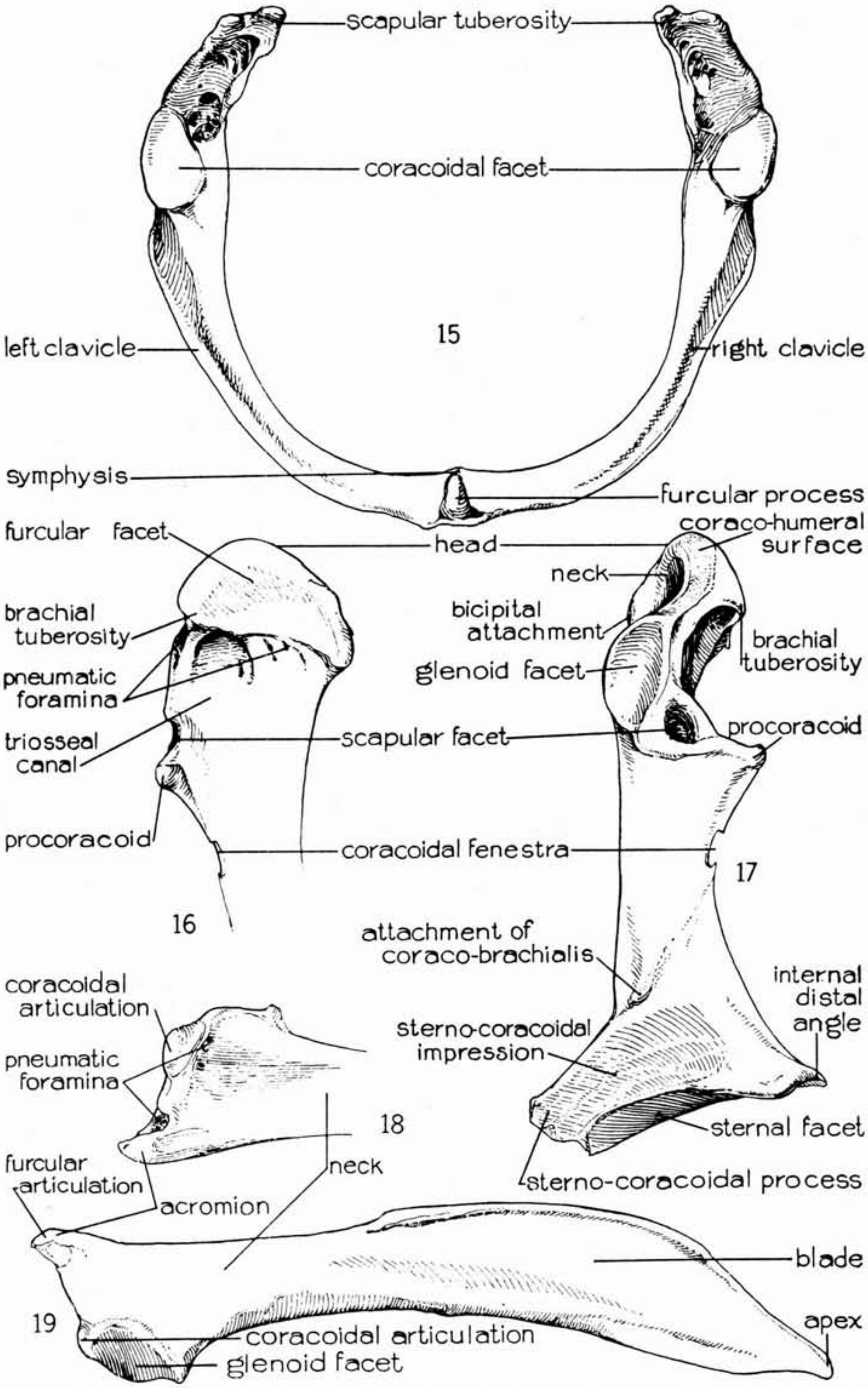
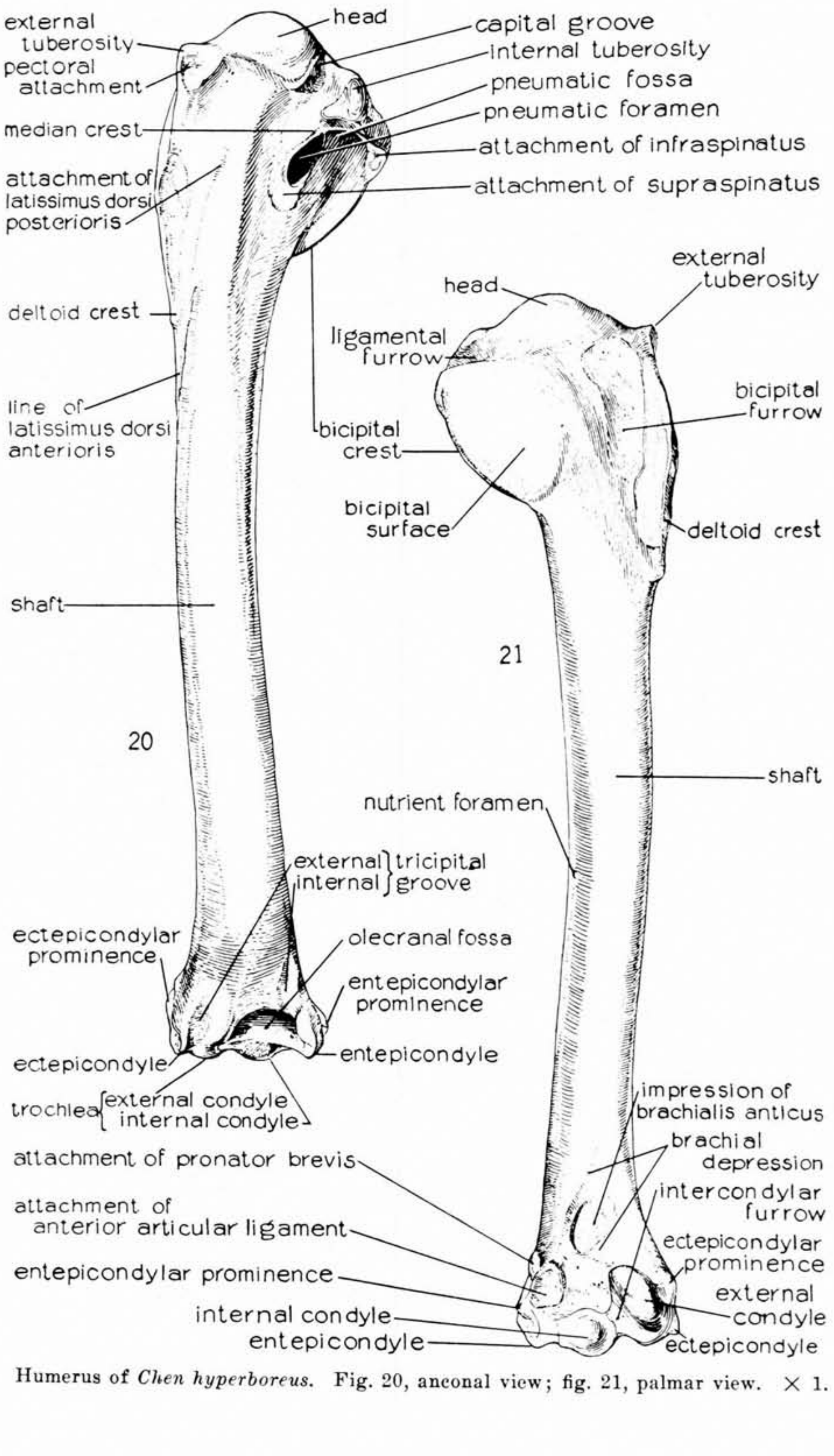
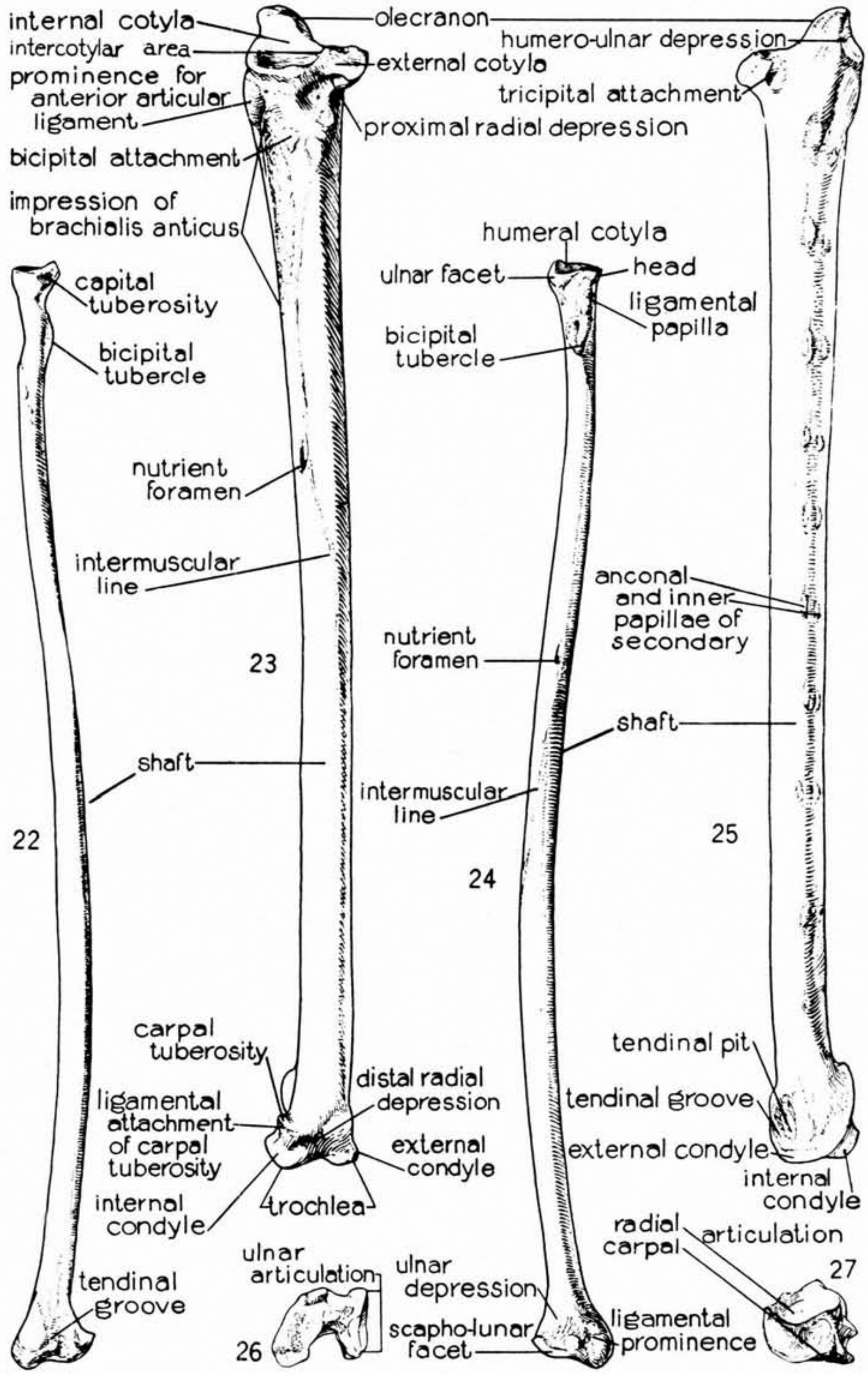
Sternum of *Chen hyperboreus*. Fig. 13, dorsal view; fig. 14, lateral view. × 1.



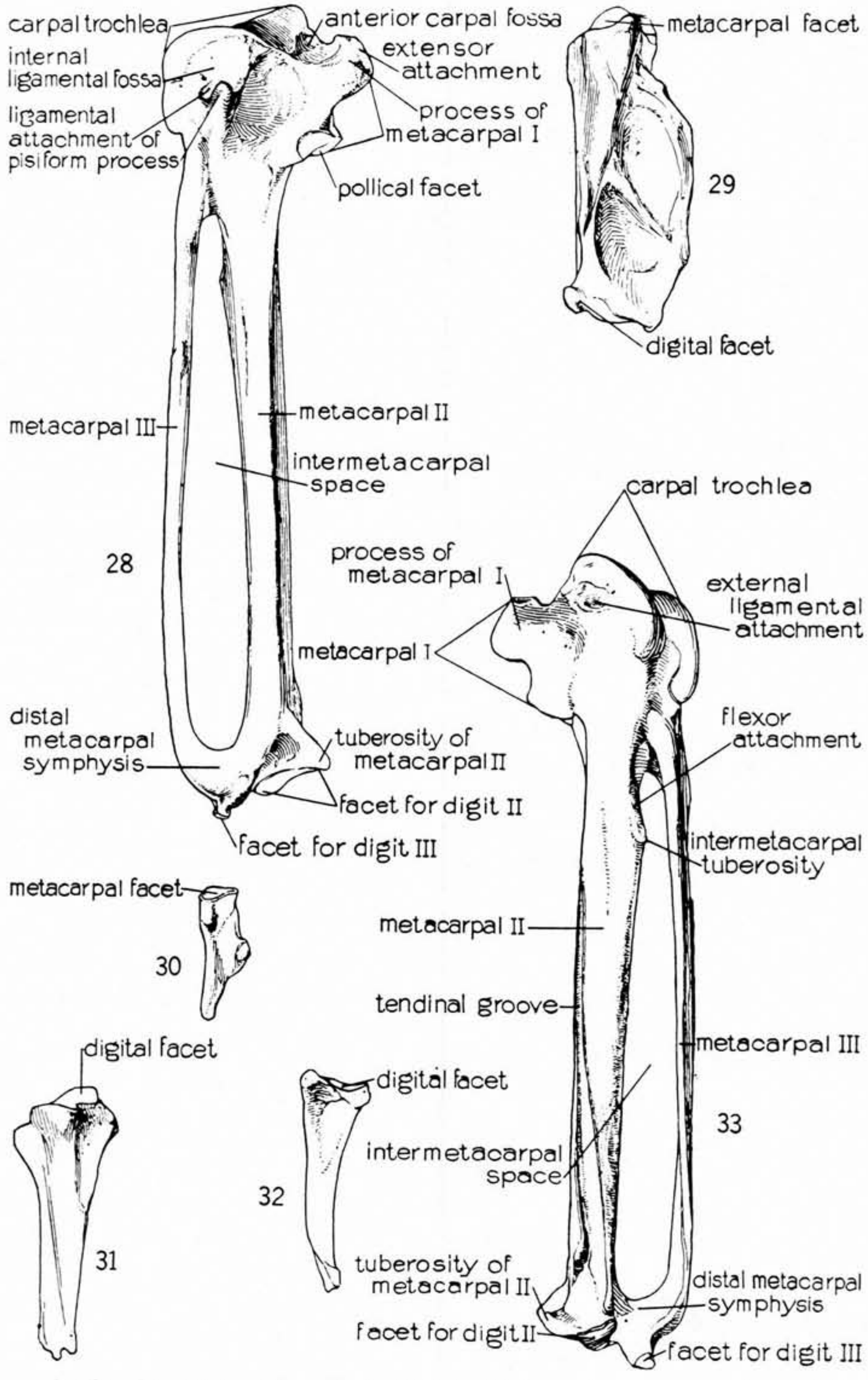
Aquila chrysaetos. Fig. 15, furcula, dorsal view; fig. 16, coracoid, internal view; fig. 17, coracoid, dorsal view; fig. 18, scapula, ventral view; fig. 19, scapula, dorsal view. × 1.



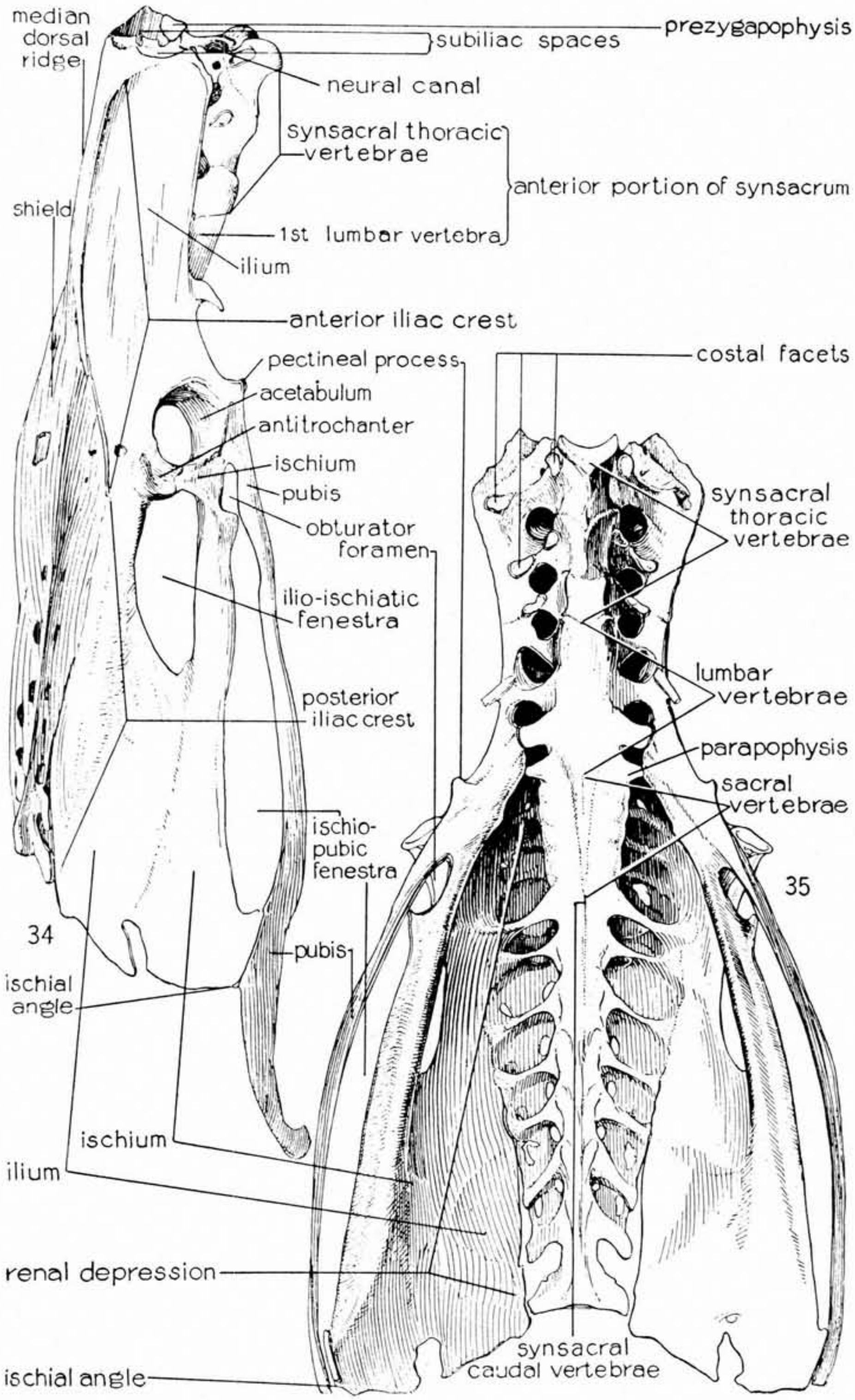
Humerus of *Chen hyperboreus*. Fig. 20, anconal view; fig. 21, palmar view. × 1.



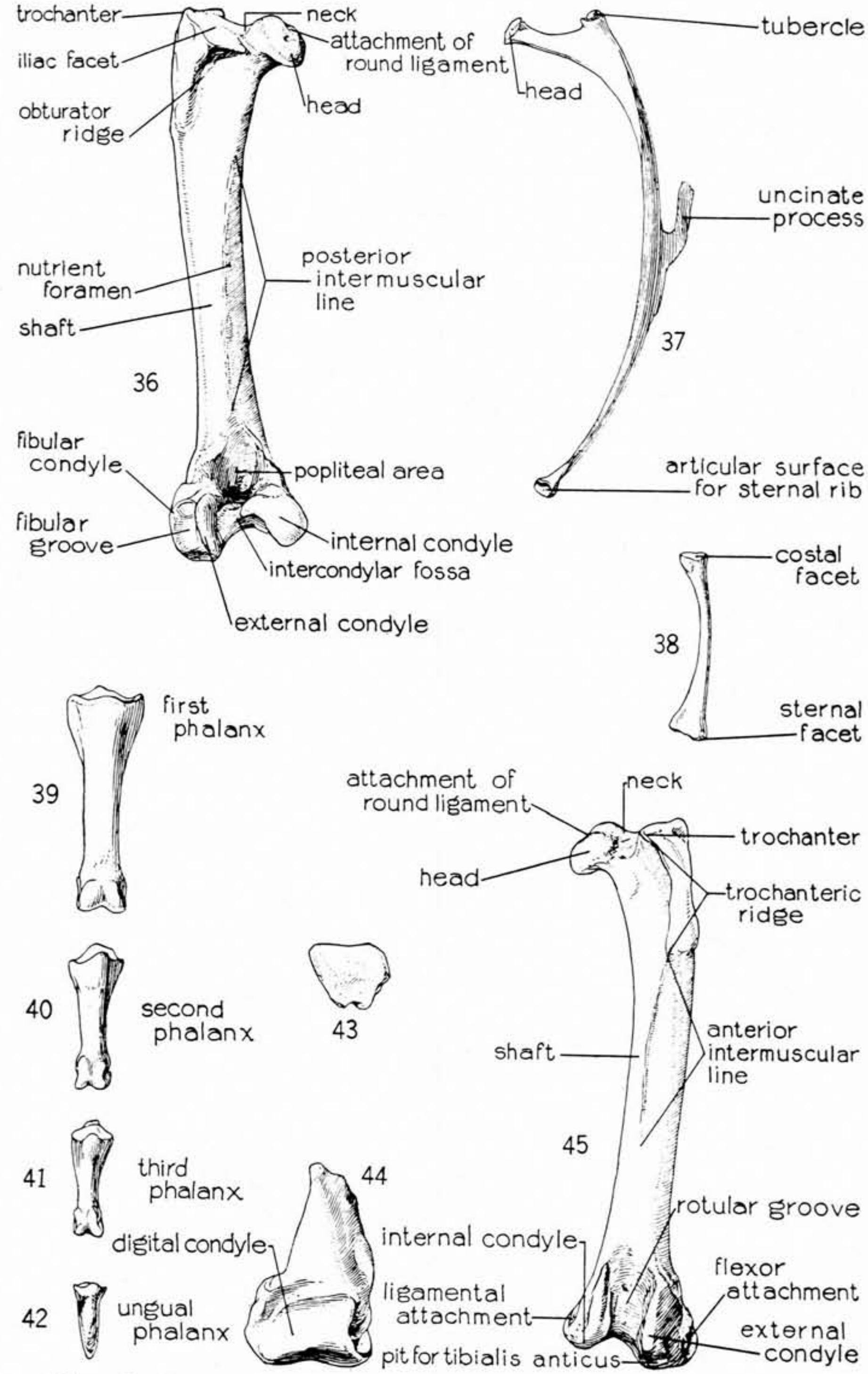
Aquila chrysaetos. **Fig. 22, radius, anconal view; fig. 23, ulna, palmar view; fig. 24, radius, palmar view; fig. 25, ulna, anconal view; fig. 26, cuneiform; fig. 27, scapholunar. Figs. 22–25 × ⅔; figs. 26–27 × 1.**



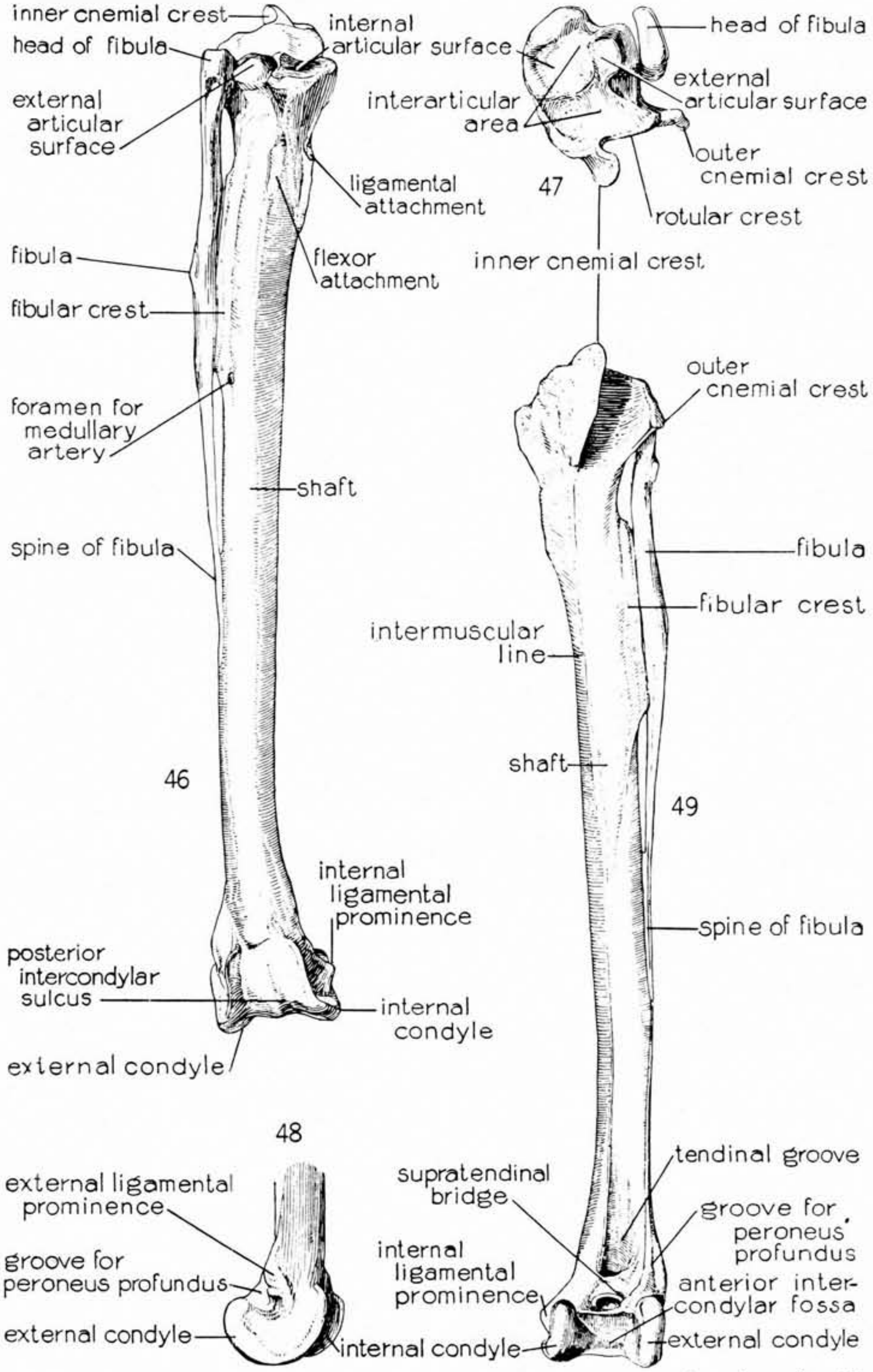
Aquila chrysaetos. **Fig.** 28, carpometacarpus, internal view. **figs.** 29–32, phalanges of manus: **fig.** 29, digit 2, phalanx 1; **fig.** 30, digit 3; **fig.** 31, pollex; **fig.** 32, digit 2, phalanx 2; **fig.** 33, carpometacarpus, external view. × 1.



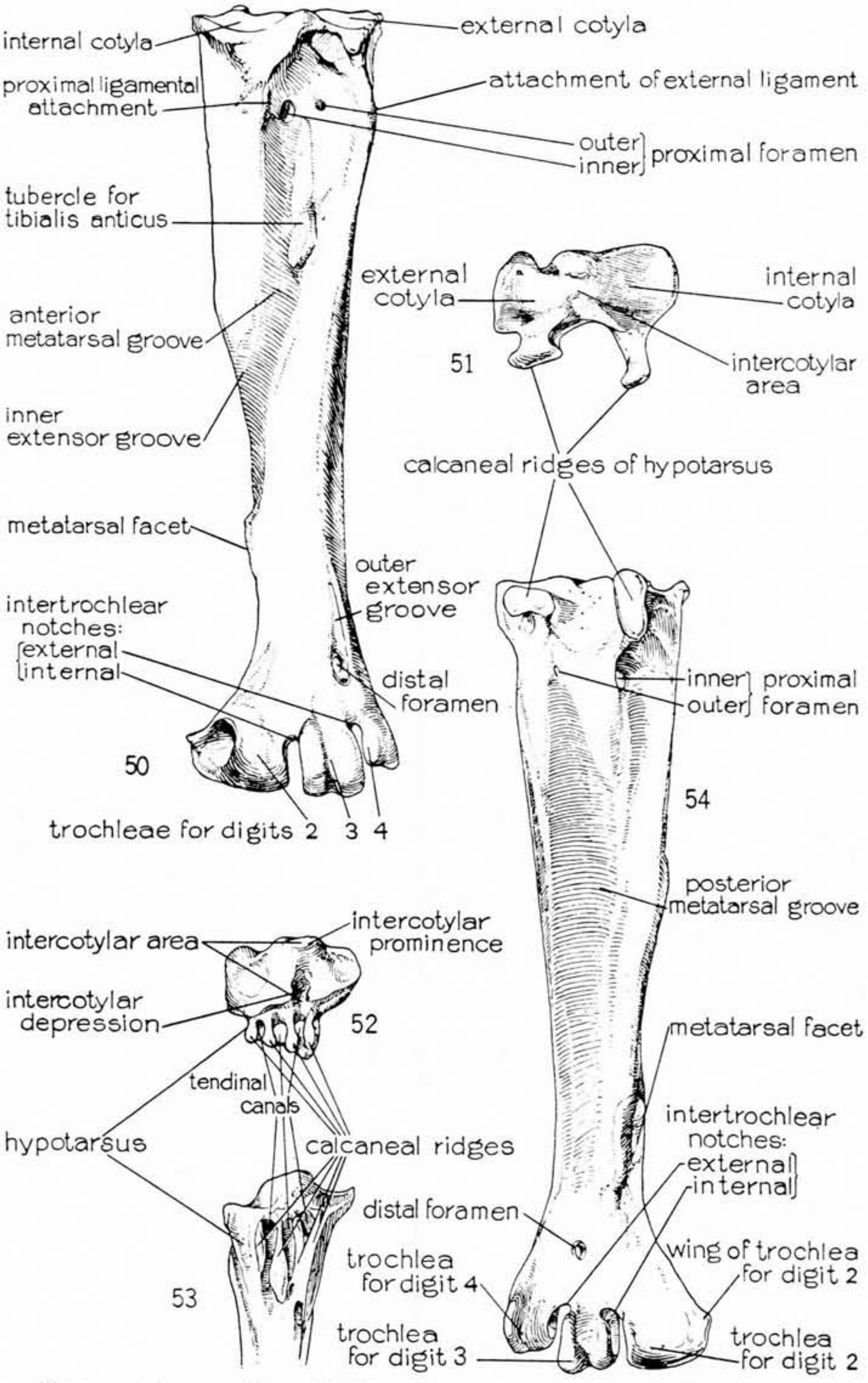
Pelvis of *Chen hyperboreus.* Fig. 34, lateral view; fig. 35, ventral view. × 1.



Figs. 36–42 and fig. 45, *Chen hyperboreus*; figs. 43–44, *Aquila chrysaetos*. Fig. 36, femur, posterior view; figs. 37–38, rib and sternal rib no. 4; figs. 39–42, digit 3 of pes; fig. 43, patella; fig. 44, metatarsal I; fig. 45, femur, anterior view. × 1.



Tibiotarsus and fibula of *Chen hyperboreus*. Fig. 46, posterior view; fig. 47, proximal end, proximal view; fig. 48, distal end, external view; fig. 49, anterior view. × 1.



Tarsometatarsus. Figs. 50, 51 and 54, *Aquila chrysaetos*; figs. 52–53, *Chen hyperboreus*. Fig. 50, anterior view; figs. 51 and 52, proximal end, proximal view; fig. 53, proximal end, posterior view; fig. 54, posterior view. × 1.

FOSSIL BIRDS AND EVOLUTION

By George Gaylord Simpson[1]

PALEORNITHOLOGY

One of the first textbooks of vertebrate paleontology, that published in 1898 by A. (later Sir Arthur) Smith Woodward devoted 14 pages, 3 percent of its text pages, to birds. It discussed particulars of only *Archaeopteryx, Hesperornis, Ichthyornis, Aepyornis* (not figured) and three moas. When I studied vertebrate paleontology at Yale in the mid-1920's the class received even shorter coverage of birds. As much time was devoted to "*Tetrapteryx,*" a "bird" that never existed, as to the two real fossil birds that were discussed. It was generally felt that fossil birds were too rare to have any great evolutionary interest beyond that engendered by *Archaeopteryx,* of which more later. That depreciative view is still sometimes encountered, but now rarely and without justification.

A decided change in this subject, and in attitudes toward it, began in the late 1920's and has been accelerating ever since. It is true that the late Alexander Wetmore published a short paper on a fossil bird as early as 1917 (Wetmore 1917) and long continued such studies, but he was primarily a neontologist and his career was centered on Recent birds. Hildegarde Howard published a long paper on a fossil bird in 1927, the start of a great career. She was certainly one of the first, perhaps the very first, to adopt paleornithology as a full-time specialty and to occupy a salaried position explicitly devoted to that speciality.

That many fossil birds were in fact known by 1930 is evident from Lambrecht's massive *Handbuch der Palaeornithologie* (1933). Even so, the first sentence of that work begins (in German), "As is known, the number of remains of fossil birds is comparatively very limited. . . ." The fossil record of birds is indeed still markedly incomplete, as is that of even such richly documented groups as, for instance, echinoderms or mammals. Nevertheless it is now far from negligible, as witness Brodkorb's *Catalogue of Fossil Birds* (1963, 1964, 1967, 1971a, 1978) and Fisher's chapter on Aves in the symposium volume on *The Fossil Record* (1969).

At present the fossil record of birds not only throws considerable light on the history of birds, a subject of great interest in itself, but also provides evidence bearing more broadly on the principles of evolution. In what follows I shall exemplify both of those aspects of the subject.

THE EARLY BIRD

A tantalizing and perhaps incorrect reference to Jurassic birds was published by Schlotheim as early as 1820. A partial but considerable skeleton of the Jurassic *Archaeopteryx* was found in 1855, but was not recognized as avian until 1970 (see Ostrom 1972). The first specimen of a Jurassic bird to be recognized as such was a splendidly preserved, nearly complete skeleton with impressions of feathers that was found in 1861 and acquired by the British Museum (Natural History). It was named and briefly described by von Meyer (1862) and more fully described by Owen (1863). Numerous other studies of that and a second specimen similar in origin have appeared since 1863. The definitive study of the British Museum specimen, made after further preparation, was by de Beer (1954a). It is interesting that this was Sir Gavin's only excursion into paleornithology. One might say that he studied this specimen only because it was there: he was at the time director of the British Museum (Natural History).

It was at once recognized, and is obvious at first sight, that *Archaeopteryx* has resemblances both to birds and to reptiles. It was early agreed that *Archaeopteryx* had evolved from some reptilian stock, but beyond that point opinions long differed. An occasional minority view was that *Archaeopteryx* was a pseudo-bird, independently derived from reptiles with no close relationship to true birds. However, there now seems to be no dissent from the majority view that it was in or near the ancestry of some, and probably of all, later birds and should itself be classed in the Aves. As to the reptilian ancestry, it was suggested as early as 1863 (Weinland) and still maintained as late as 1950 (Petronievics) that *Archaeopteryx* was derived from some lacertilian stock. Owen (1874) hinted, although not clearly in evolutionary terms, at a pterosaur ancestry. Neither of those views is tenable in the light of later studies. Abel (1919) suggested derivation from a pseudosuchian, but possibly from some dinosaur itself evolved from a pseudosuchian (or other early thecodont). Heilmann (1926) more positively endorsed derivation from a pseudosuchian. T.H. Huxley (1868), somewhat vaguely, and Marsh (1877) and others following him, more positively, supported descent from some early dinosaurs.

There has long been a strong consensus, now virtually unanimous, that birds, including *Archaeopteryx,* evolved either from a dinosaurian (theropod) stock, or from a common ancestry with such a stock but within prior thecodonts. Ostrom (e.g., 1975), the most recent to study this question in depth, is insistent on a dinosaurian origin. He considers the skeleton of *Archaeopteryx* more dinosaur-like than bird-like, but continues to classify the genus as an ancestral, or near-ancestral, bird.

Whether birds arose from dinosaurs or from the immediate common ancestry of birds and dinosaurs is a phylogenetic detail of no great importance from a broader view of evolutionary

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Contrib. Sci. Natur. Hist. Mus. Los Angeles County. 1980. **330**:3–8.

Table 1. Some data on first appearances of families of birds in the fossil record, based mainly on Fisher (1967).

Geologic Period or Epoch	Number of First Known Appearances	Percent Extinct before the Holocene	Percent Surviving into the Holocene
Jurassic	1	100	0
Cretaceous	12	75	25
Paleocene	3	66.7	33.3
Eocene	41	31.7	68.3
Oligocene	18	38.9	61.1
Miocene	24	25	75
Pliocene	9	0	100
Pleistocene	38	2.6	97.4
Holocene	54	0	100

theory. In either case it is clear that *Archaeopteryx* stands in an intermediate position between the classes Reptilia and Aves. During the transition from one class to another, evolution may have been, and quite likely was, accelerated, but there was a transition, not a saltation as has from time to time been claimed for the origin of taxa at upper hierarchic levels. There are no known instances of such origins that cannot have been transitional, many known cases, of which this is only one, in which the origin was almost certainly transitional, and no known cases in which the evidence makes saltation more probable. The old saw that the first bird was born from a reptile's egg is not true.

That is the most important theoretical bearing of the early bird, but it has another also of some importance. When there is a transition from one high taxonomic category to another there are two extreme theoretical possibilities, although something between the two extremes is also quite possible. At one extreme, all characteristics of the ancestral form may evolve uniformly into the different characteristics of the descendant, so that an animal like *Archaeopteryx* would be in all respects intermediate between one high taxon, in this case the Class Reptilia, and another, here the Class Aves. As a matter of fact *Archaeopteryx* is not intermediate in that sense. Many of its characters had changed hardly at all from the reptilian grade, although I think that Ostrom, as previously cited, has somewhat overstated that case. On the other hand, some characters of that genus were already completely avian, notably the furcula, the presence of feathers, and their arrangement on the wing.

De Beer (1954a) did not discuss just this point in his monograph on the London specimen, but he did in an address to the British Association for the Advancement of Science (de Beer 1954b). He proposed the term "mosaic evolution" for the apparently disharmonious sort of transition exemplified in *Archaeopteryx*. He also gave other examples, and many more have been pointed out since then. In fact it had long been recognized, although not always so clearly, that different characteristics of organisms often, indeed usually, evolve at quite different rates even within a single lineage. (Although I was not the first to notice this, I did clearly state it in 1944, 10 years before the restatement by de Beer.) De Beer's term is apt and is a handy designation for this phenomenon. De Beer did not himself claim that his observation of the phenomenon was original, although some subsequent users of the term have mistakenly ascribed the principle, and not only the term, to him.

Two other points involving *Archaeopteryx* are to be mentioned here only briefly. It is fairly obvious that *Archaeopteryx* could not have been capable of long, sustained flight in the manner of most modern birds. There was, however, a clear consensus that it was capable of brief gliding or leaping flight and that its strongly feathered forelimbs were a stage in the evolution of sustained flight. Recently, however, Ostrom (1976) has maintained that the origin of those feathered forelimbs had nothing to do with flight but were adaptations of a running animal for garnering insects. If that were true, those forelimbs would be only adventitiously preadapted for flight. I do not pretend to authority on this point, but I do find Ostrom's hypothesis incredibly bizarre. (See Feduccia 1979—note added after completion of this manuscript.)

The other point is that it has several times been suggested that various birds without aerial flight (although many of them with wings) were primarily flightless either because they evolved from reptiles independently of true Aves or because the ancestral Aves were flightless (for example, Lowe 1944, and earlier papers there cited). With special reference to penguins, but incidentally to other supposedly flightless birds, I (Simpson 1946) strongly opposed that view, and I do not know of any more recent adherence to it.

BITS OF AN OUTLINE OF HISTORY

There have been several fairly recent reviews of the whole history of birds, most notably that by Brodkorb (1971b). I am not capable of writing a review in equal or greater depth and have no intention of trying. There are, however, some points bearing on evolutionary principles and on the interpretation of the fossil record that suggest brief comment here.

Some data on the first appearances of families of birds are given in Table 1. I have based these on Fisher (1967), primarily because Brodkorb's catalogue was not complete when this paper was written. Even now the earlier parts (at least Brodkorb 1963, 1964, and 1967) are out of date. The data from Fisher, more complete than Brodkorb's when this paper was written, seem to be sufficient for the general points here made.

It is not surprising that the percentage of pre-Holocene extinctions decreases, and that of survival into the Holocene increases almost regularly from Jurassic to Holocene. (A few families known only from the Holocene but now extinct are here counted as Holocene survivals.) The only somewhat evident irregularity is in the Oligocene, and this is probably a sampling error. For one thing, the Oligocene was shorter than either the Eocene or the Miocene, and so would have fewer first appearances even if the rate per annum were constant.

The very high numbers of first appearances in the Pleistocene and Holocene are a measure of the incompleteness of the record. It is highly improbable that these families actually originated in either of those epochs. Thus with no probable and few possible exceptions, their pre-Pleistocene members simply have not yet been found, to put the matter optimistically. To put it pessimistically, in many instances pre-Pleistocene representatives may not exist as accessible fossils. (Even for vertebrates it is certain that not all species or genera, probable that not all families, and possible that not all orders were fossilized and are now present in rocks accessible for exploration.)

It is a reasonable conclusion from these figures and from the more detailed data on which they are based that most and perhaps all of the families of birds that have ever existed, and hence of course those now surviving, had arisen by the end of the Miocene. That agrees with the well-informed opinion of Brodkorb (1971b:43), who wrote that, "By the end of the Miocene all of the nonpasserine families were probably established, as well as most, if not all, of the passerines." He then estimated that there were about 155 families extant in the Miocene, the number being reduced moderately to 148 in the Holocene.

For comparison, I have given in Table 2 similar data for Mammalia, a class with a better but still quite incomplete fossil record. The figures are tentative only, because there is no recent and reliable listing of all known mammalian families and their distribution in the Cenozoic, although Lillegraven (1972) has published graphs based on a fairly recent tabulation. (There is one by Lillegraven, Lindsay, and Simpson, as yet unpublished, for the Mesozoic.) My arrangement is conservative, with fewer families than are now sometimes recognized in the Tertiary, but I believe that the pattern is significant. Even so my arrangement for mammals has many more families (259) than Fisher's for birds (200). The patterns are similar in some respects but strikingly different in others. A considerable number of bird families first known in the Cretaceous, Paleocene, and Eocene—32 families or 57 percent of those first appearing during those times—survived into the Holocene. For mammals the corresponding figures are 116 families and 26.7 percent. Both proportionately and absolutely, many more mammalian than bird families first appear in the record at those times, but fewer of them survived into the Holocene. For both classes most of the Holocene families had appeared by the end of the Miocene, but some of the mammalian families probably did become differentiated in the Pliocene whereas it is not clear that any bird families did. In both cases it is unlikely that any family emerged after the Pliocene. The much lower numbers and percentages of first appearances of mammalian than of bird families in the Pleistocene and Recent is evidence that the fossil record for mammals, although still incomplete, is better than that for birds.

As Brodkorb (1971b) has pointed out, more living families of birds appear in the record for the Eocene than at any other time. (It is understood that comparison with the higher numbers for the Pleistocene and Holocene is not valid.) For mammals there is a marked difference: the greatest number of living families appear in the record for the Miocene. There are in fact many more Miocene first appearances than Pleistocene or Holocene. As relatively few Eocene mammalian families are still living, it is clear that there has been a much more marked faunal turnover since the Eocene for mammals than for birds.

The bird record is strongly biased both taxonomically and geographically. The most striking taxonomic bias is that relatively far fewer passeriform families than nonpasseriform families are known before the Pleistocene. On Fisher's data only 22.8 percent of recognized passeriform families are known before the Pleistocene but for nonpasseriforms the figure is 67 percent. That may be a sampling bias, caused in part by nonpasseriforms (such as many shore birds) being more likely to be preserved in sediments, by a higher proportion of nonpasseriforms in regions that have been sampled, or by smaller average size of passeriforms making them harder to find and identify. However it is also evident that the differentiation of passeriform families probably occurred, on an average overall, at later dates than for nonpasseriforms.

Table 2. Some data on first appearances of families of mammals in the fossil record.

Geological Period or Epoch	Number of First Known Appearances	Percent Extinct before the Holocene	Percent Surviving into the Holocene
Rhaeto-Lias	4	100	0
Jurassic	11	100	0
Cretaceous	19	94.7	5.3
Paleocene	33	100	0
Eocene	63	82.5	17.5
Oligocene	44	56.8	43.2
Miocene	38	28.9	71.1
Pliocene	21	9.5	90.5
Pleistocene	7	0	100
Holocene	26	0	100

The geographic bias largely, although not entirely, follows the intensity of paleontological field work. Fossil birds are fairly well known in North America and Europe but less so in South America, Asia, Africa, and Australia. Yet even in Australia there is a fair sampling from the Miocene onward, as was recently tabulated by Rich (1975). The evidence suggests that by mid-Miocene, at latest, the Australian fauna was fairly modernized and largely endemic. Virtually all the known fossils are nonpasseriform. From Antarctica some fossil penguins are known, but no deposits likely to contain nonmarine birds have yet been found.

EVIDENCE FOR SUCCESSIVE RADIATIONS

Descriptions by Marsh (1872, 1880) of *Hesperornis* and *Ichthyornis,* supposedly toothed birds, created a sensation and these have been the most discussed fossil birds except *Archaeopteryx*. It was already known that *Archaeopteryx* had teeth, but Marsh's "Odontornithes" were much later, and some authorities did not consider *Archaeopteryx* wholly (or at all) a bird. More recently Gregory (1952) suggested that, although *Hesperornis* had teeth, *Ichthyornis* probably did not. Bock (1969) still later questioned whether *Hesperornis* had teeth. Brodkorb (1971b) attacked "the fable of the toothed birds." The fable was simply the claim that *all* Mesozoic birds had teeth. In fact both *Hesperornis* and *Ichthyornis* did have teeth (Gingerich 1972, 1973; Martin and Stewart 1977). Although possibly tooth-bearing parts are not known in the likewise Cretaceous genera *Baptornis* (referred by Brodkorb 1963 to the Podicipediformes), *Enaliornis* (referred by Brodkorb to the Gaviiformes), or *Neogaeornis* (referred by Brodkorb to the Podicipediformes), Martin and Tate (1976) have established that these genera, too, probably belong in the Hesperornithiformes.

Added indication of the archaic nature of the genera listed in the preceding paragraph is given by evidence that the skull of *Hesperornis* was in fact palaeognathous (Gingerich 1973, 1976) although faulty reconstruction had led to belief that it was neognathous. Although the skull structure of *Archaeopteryx* is not known in clear detail, Gingerich has also marshalled evidence that a palaeognathous skull was probably ancestral for birds in general, and hence probably was present in *Archaeopteryx*. (I am, however, informed that Martin and Whetstone, in a study not published when this paper went to press, deny that *Hesperornis* was palaeognathous, which would also cast doubt on the possible palaeognathy of *Archaeopteryx*.)

Thus in the Cretaceous there was a group of archaic birds apparently sharing ancestral characters, although divergent to the ordinal level in derived characters. Among the Hesperornithiformes and the Ichthyornithiformes long known, some, at least, and possibly all were palaeognathous, and some and possibly all retained teeth. To them may now be added *Gobiopteryx* from the late Cretaceous of Mongolia (Elżanowski 1977). It, too, was palaeognathous, but it was toothless. Elżanowski proposed for it a new order, Gobiopterygiformes, but it might well be put in the still living order Casuariiformes, or the Struthioniformes if, as has been defended by Bock (1963) among others, all the ratites were put in one order. (The definition of such an order becomes difficult if some palaeognathous birds are excluded from it.) Brodkorb (1978:224) has expressed his belief that *Gobiopteryx* is not a bird, but a small dinosaur.

The most economical hypothesis is that the living palaeognathous birds, the ratites (whether classified as one order or as up to six) and the tinamous, are survivors of an archaic radiation. Most of the known Mesozoic members of that radiation were aquatic or at least littoral and most were found in marine rocks. Of earlier known members of the radiation, *Archaeopteryx* and *Ichthyornis* were most likely to have been land birds, but they have been found only in definitely marine beds. The known later, Eocene to Holocene, palaeognathous birds are land birds; all but the tinamous are flightless, and the tinamous are poor fliers.

Thus we can return, with Gingerich (1976), to the essence of views already expressed by T.H. Huxley (1868) and by Marsh (1880) long ago. The palaeognathous birds are the relics ("waifs and strays" of Huxley) from an archaic (mainly Cretaceous) radiation of the Aves.

Although Brodkorb's view that almost all the known Cretaceous birds were referable to, or near the ancestry of, Cenozoic neognathous birds is an overstatement, it seems established that, near the end of the Cretaceous, some were (Brodkorb 1976). Because of the bias of sampled environments, the known Cretaceous members of probably neognathous groups are almost all aquatic, marine, or shore birds. They strongly suggest that a major radiation of neognathous nonpasseriforms was under way before the end of the Cretaceous, reaching its height in the early Cenozoic. Starting within that radiation, one basic line, that of the passeriforms, underwent its own radiation from mid-Cenozoic to Holocene and became the dominant group in later Cenozoic and Recent avifaunas.

A WORD ABOUT PENGUINS

The oldest known penguins are late Eocene in age (not early Eocene, as indicated by Fisher 1967; Fisher also errs in listing *Palaeeudyptes marplesi* as a neospecies). At that time they already had all the derived characteristics of the family Spheniscidae as a whole. Some, at least, of the known late Eocene through Miocene species had a few characters that seem to have been more primitive than recent penguins, but at the generic level they also had derived characters that make them all quite distinct from any recent genus. Some of them, even in the late Eocene, had quite specialized generic characters. It is unlikely that any of the known forms of those ages were closely related to recent penguins at the generic level, and those that are adequately known were probably not ancestral to known post-Miocene penguins. Only in the late Pliocene of New Zealand do two species occur in the known record that are close to, and have been referred to, living genera: *Pygoscelis* and *Aptenodytes*. (On those two see Simpson 1972, and on fossil penguins in general Simpson 1975, and earlier publications there cited; for a less technical discussion see also Simpson 1976.) It is curious that those two genera now live much farther south than where their known fossil species were found, although by the late Pliocene New Zealand must have been in nearly the same latitudes as now. No pre-Pleistocene fossils are known for the genera now breeding in New Zealand: *Megadyptes, Eudyptes,* and *Eudyptula*.

The family Spheniscidae and order Sphenisciformes must have evolved before the late Eocene when they first appear in the record, and some, if not all, Holocene genera must have had distinguishable ancestors before the late Pliocene. As penguins are marine and littoral, they would seem well-suited for preservation as fossils. Nevertheless two special circumstances make the almost complete lack of ancestral or transitional sequences explicable. First, penguins are predominantly insular. One genus each now occurs on the coasts of three continents: Africa and South America (*Spheniscus*), and Australia (*Eudyptula*). Only two genera (*Aptenodytes* and *Pygoscelis*) occur in continental Antarctica, where, furthermore, no appropriate fossil-bearing post-Eocene rocks are known. All six living genera are now much more common on islands than on continents, and twelve of the (nominally) sixteen to eighteen living species are almost or quite confined to islands when ashore anywhere. The prolific polytypy of the group now, and even more its speciation in the past, are evidently the result of the isolation of island populations, with some subsequent dispersal. The islands on which ancestral speciation leading to later genera occurred probably no longer exist for the older part of the record, at least, and for the later part those that exist are not known to have fossiliferous rocks of appropriate ages. A second point is that all known fossil penguins are well within the geographic ranges of Recent penguins, and the whole order has probably always been almost entirely restricted to areas now in the Southern Hemisphere. But the known fossil record of birds in general in that hemisphere is exceptionally poor. It is surprising that so many, rather than so few, fossil penguins are known.

Until recently penguins were usually considered particularly primitive birds. That view is evident even in the the fairly recent compendious summary by Fisher previously cited. Penguins are there listed in the heart of orders belonging to the earliest radiation, between the Ichthyornithiformes and the Struthioniformes. That and similar arrangements may be a not wholly conscious hangover from the speculation that penguins are primitively (ancestrally) flightless. In fact they are carinate and neognathous and they fly with great power, but in water rather than in air. They quite surely had ancestors that did fly in air. The picture of avian evolution here adopted is a succession of three radiations of differing character and scope: ancient and largely or wholly palaeognathous, neognathous nonpasseriform, and neognathous passeriform. It is clear where penguins belong in that scheme: in the neognathous nonpasseriform radiation. Within that group their derived characters are unique in detail and association. They make the penguins among the most specialized birds. Only in some of the Alcidae (including Mancallinae), another branch of the neognathous nonpasseriform radiation, did some similar derived characters evolve (but see Olson and Hasegawa 1979; Olson this vol.—Ed.). That development was clearly independent and convergent on the part of sea birds that were geographic, Northern Hemisphere, vicars of the Southern Hemisphere penguins.

NOTE

The manuscript was written early in 1978. Although a few changes have been made since that time, it has not been possible to update fully.

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PHYLOGENETIC THEORY AND METHODOLOGY IN AVIAN PALEONTOLOGY: A CRITICAL APPRAISAL

By Joel Cracraft[1]

ABSTRACT: The thesis of this paper is that the application of the theory and method of cladistic analysis (phylogenetic systematics) will greatly improve systematic practices within avian paleontology. Specifically, cladistic analysis will (1) facilitate the formulation of more precise phylogenetic hypotheses of Recent taxa, and these in turn will clarify the array of hypotheses that must be considered when analyzing the systematic position of fossil taxa; (2) draw attention to the concept that phylogenetic relationships are postulated on the basis of shared derived characters and to the realization that the morphology of fossil taxa will have to be studied in these terms; and (3) de-emphasize the importance of considering intermediate taxa as possible ancestors and focus attention instead on assessing their cladistic relationships. The major methodological problem in avian paleontology is the belief that relationships can be determined by some measure of overall similarity. Cladistic theory and methodology provides a solution to this problem: similarity must be partitioned into primitive and derived conditions at each hierarchical level. Consequently, there is a nested pattern of derived similarities for any set of taxa, and the primary methodological goal of systematics is the search for this pattern.

There has been scant discussion about the theory and method of phylogenetic analysis in avian paleontology. Avian paleontologists seem to operate comfortably within the conceptual framework established by post-Darwinian vertebrate and invertebrate paleontology. In general this can be characterized by the assumption that the phylogenetic process is slow and gradual, with species being arbitrary segments of an evolutionary continuum. This transformational or gradualistic philosophy engenders the view that phylogenetic analysis is primarily an empirical endeavor, with fossils our only recourse to reconstructing the history of life:

> The morphology, physiology, zoogeography, and behavior of living birds tempt us to deduce phylogenetic relationships, but without paleontological support such conclusions must remain hypothetical. Only the fossil record will teach us, eventually, what has in fact happened. (Brodkorb 1971:20)

As mentioned, the gradualistic philosophy constrains our approach to phylogenetic methodology, and manifestations of this philosophy are common in the literature of avian paleontology and phylogeny. Because fossil data are often considered superior to neontological data and because it is assumed that fossils are the best evidence for discerning the geometry of phylogeny, paleontologists frequently do not attempt to analyze the relationships of fossil taxa within some prior phylogenetic hypothesis of Recent taxa. The time dimension itself is emphasized, and fossil taxa, simply because of their age, serve as the basis for speculations about morphological transformation sequences or changes in geographical distribution; such analyses are seldom, if ever, carried out within the context of testing alternative phylogenetic hypotheses. Finally, the gradualistic philosophy emphasizes a search for ancestors. Unfortunately, it is doubtful whether a single case within the literature of avian paleontology approaches the problem of the identification of ancestral taxa within a testable framework. On the contrary, ancestors are specified either because they occur earlier in time and seem to possess some primitive features or because they seem to be morphologically intermediate between two or more Recent taxa. In this paper I shall outline some theoretical aspects of phylogenetic analysis that are currently being discussed in the systematic literature, discuss their implications for paleontological analysis within ornithology, and apply them to a critique of some current paleontological practices in order to suggest that theorectical ideas can have a significant impact on real-world data analysis. One of my conclusions is that, if practicing paleontologists paid more attention to theory, their methodology would be improved substantially.

HYPOTHESES ABOUT PHYLOGENETIC PATTERN

THE NATURE AND EXPECTATION OF PATTERN

Species taxa can be hypothesized to be discrete evolutionary units in space and time if it is assumed that the period of differentiation is itself short relative to the period of species existence. The evidence for this seems relatively strong (Eldredge and Gould 1972; Gould and Eldredge 1977; Stanley 1978). Methodologically, the majority of fossil vertebrate

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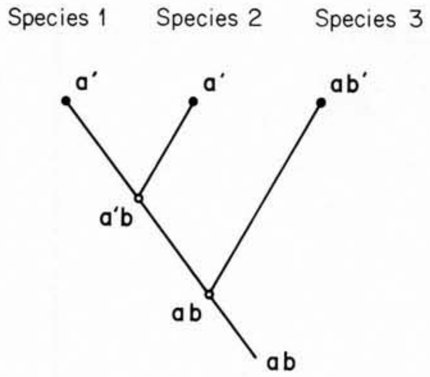

Figure 1. The expectation that evolutionary novelties (derived characters) exhibit a nested pattern can be assumed from evolutionary theory. Species 1 and 2 are hierarchically nested within a larger group (species 1 + species 2 + species 3) on the basis of sharing a derived character, a'. No other aspect of morphological comparison that is used to form nested sets of taxa seems consistent with evolutionary theory.

species taxa, and certainly nearly all those of birds, can be viewed as discrete. If so, then the adoption of discrete species in phylogenetic analysis, particularly within paleornithology, would seem to be logically and empirically well-founded.

A proper analysis of *phylogenetic pattern* is a prerequisite for all subsequent discussion about the nature of evolutionary trees. By phylogenetic pattern, I mean the nested pattern of evolutionary novelties (derived characters) exhibited by the taxa in question. Indeed, the existence of such a nested pattern might be taken as a fundamental deduction of the theory of evolution (Fig. 1).

The pattern of nested evolutionary novelties for any group of taxa must be inferred as it is not subject to direct empirical investigation. Hypotheses about this pattern are termed *cladograms*; this usage of cladogram need not refer specifically to a statement about evolutionary history, as will be discussed below.

CONSTRUCTING CLADISTIC HYPOTHESES

The methods used to construct cladograms have been discussed in considerable detail by various workers (Hennig 1966; Schaeffer et al. 1972; Cracraft 1972, 1974a; Wiley 1975; Eldredge 1979; Eldredge and Tattersall 1975; Eldredge and Cracraft 1980; Bonde 1977; Gaffney 1979), so only the salient features will be mentioned here.

Clearly, the central methodological problem of cladistic analysis is the identification of evolutionary novelties. Some paleornithologists have questioned our ability to recognize derived conditions by comparative analysis:

> I doubt that a methodology exists for actually determining primitive-derived sequences in more than a handful of cases in the entire class Aves. In comparisons across broad groups of birds it may be impossible to determine unequivocally which character states are primitive and which are derived. . . . (Feduccia 1976:598)

But such an extreme position is clearly unjustified, for many of the defining characters of countless avian taxa, at all taxonomic levels, are almost certainly derived, despite the fact that previous workers have not presented extensive corroborative evidence. Within a cladistic view of phylogeny reconstruction, the issue is not whether we can "establish unequivocally" the polarity (i.e., whether primitive or derived) of observed similarities (Feduccia 1976:598; 1977:20), for clearly scientific analysis cannot establish such issues with certainty. This is not to deny that evidence for character polarity may be difficult, or perhaps impossible, to gather in individual cases. Nevertheless, the methods of cladistic analysis seek to establish hypotheses about character polarity and then use these hypotheses to evaluate alternative phylogenetic hypotheses; these latter hypotheses, in turn, tell us something about our estimations of character phylogeny.

Perhaps the most critical cognitive issue in the theory of phylogeny reconstruction is the realization that monophyletic groups can be defined only by shared derived characters (synapomorphies). As was illustrated earlier (Fig. 1), this conclusion is a simple expectation of evolutionary theory. If so, then difficulties in determining polarity would seem to be beside the point, for no other type of similarity can define monophyletic taxa and be, at the same time, theoretically compatible with what we know of the evolutionary process. In cases of difficulty, therefore, it would appear we simply have to work harder.

Three types of data traditionally have been recommended as being useful in determining polarity: ontogenetic, paleontological, and the comparative distribution of homologous characters. Because this discussion is primarily concerned with the analysis of fossil material, ontogenetic data will not be considered further (see Nelson 1978).

Because of the importance often attached to paleontology as the final arbiter of phylogenetic questions (e.g., the quote of Brodkorb above), data from fossils traditionally have been considered important in postulating polarity sequences. Those characters occurring earlier in the stratigraphic record are thought to be primitive relative to those occurring later. That primitive characters must occur earlier in time cannot be denied. The relevant question is whether the *observed* distribution of characters in the fossil record accurately parallels character phylogeny. The answer is that we cannot have *a priori* knowledge about the degree to which this parallel exists. Relatively greater confidence in the parallel traditionally has existed when the fossil record is dense or when the alternative characters are distributed stratigraphically in widely separated time intervals. But most vertebrate fossil records, and certainly that of birds, do not fall into the categories set by these extremes. It has been repeatedly stated in the literature that there is no theoretical reason why we should not expect derived characters to occur sometimes in earlier strata than primitive conditions: indeed, if species extinctions or survival, probability of fossilization, and probability of recovery by paleontologists are all statistically independent of whether the species possessed a primitive or derived condition for a given feature, then this expectation must be admitted. Thus, there is no reason why the reverse order of discovery cannot be of fairly common occurrence.

One problem with paleontological inquiry in this regard is that the fossil record is too often assumed to give us an empirical picture of history. The pattern of the fossil record—the distribution of taxa and characters in space and time—must be evaluated critically. Paleontological data can be used to hypothesize polarity sequences, but then these hypotheses need to be evaluated by comparative "out-group" procedures. What must be avoided is axiomatic acceptance of fossil data as a true picture of character phylogeny.

Without question, comparative analysis of taxa offers the best source of data for inferring character phylogeny. As mentioned earlier, the justification for comparative analysis follows from the expectation that evolutionary novelties (derived characters) are nested. Thus, for a given character transformation, a condition postulated to be primitive within a group, say AB, may characterize (define) a taxonomic group (ABC) broader than, and including, group AB, which itself must be defined by a derived condition of a second character. What this means is that all postulated homologies are derived (synapomorphous) at one level and primitive (symplesiomorphous) at all lower levels. Out-group comparison has been discussed extensively in the literature (see references cited above). Only one comment is necessary here: out-group comparison does not necessitate definitive knowledge or acceptance of a higher-level phylogeny, because such phylogenetic hypotheses are themselves open to critical testing (Wiley 1975; Gaffney 1979).

Once primitive-derived sequences are postulated, one or more phylogenetic hypotheses are usually suggested. It is rare for a single phylogenetic hypothesis to be compatible with all the polarity sequences. The problem then becomes one of evaluating alternative cladistic hypotheses.

EVALUATION OF CLADISTIC HYPOTHESES

If a postulated synapomorphy is consistent or congruent with a proposed cladistic hypothesis, say A + B, then that synapomorphy conflicts or is incongruent with alternative hypotheses such as A + C, B + C, A + D, B + D. . . . The goal of cladistic analysis is to find that hypothesis with the fewest conflicts, or expressed in more affirmative terms, to find that hypothesis which best accounts for the pattern of nested synapomorphy. It is necessary to minimize conflicts in synapomorphy because for each conflict an explanation must be found, and there seem to be only two: (1) the similarity is homologous, but not a synapomorph; therefore, it is a shared primitive similarity (a symplesiomorph), in which case it is not relevant in evaluating the alternative cladistic hypotheses at this hierarchical level, or (2) the similarity is not homologous in the first place and must be explained as a convergence. To invoke convergence as an explanation of a conflict in a given cladistic hypothesis is *ad hoc* for that hypothesis because we must therefore accept that the taxa sharing the similarity are not monophyletic, i.e., we must assume some other cladistic hypothesis to be true. Thus, the choice of the cladistic hypothesis that minimizes conflicts in postulated convergences is simply a method of minimizing *ad hoc* assumptions.

This discussion emphasizes the reciprocal nature of testing cladistic hypotheses and evaluating hypotheses of character phylogeny. Although character phylogenies are postulated on the basis of comparative data, their ultimate evaluation rests on the extent to which they are nested by a cladistic hypothesis. If, within a specific cladistic hypothesis, an observed character does not define a set of taxa at some hierarchical level, then that character cannot be interpreted as derived. On the other hand, within the framework of an alternative hypothesis, that character may be interpreted as derived.

The major problems within ornithological systematics and paleontology with regard to phylogenetic reasoning are (1) hypotheses of relationships are seldom precisely stated, and the taxa being analyzed are not always strictly monophyletic, or assumed to be (see Example 1 below), and (2) these hypotheses are frequently not evaluated by derived characters (see Examples 1 and 2 below). More often than not, decisions about relationships are based on overall resemblance, or the characters used to unite groups are primitive, in which case the argument for relationships is severely weakened. Finally, it is often not appreciated that the phylogenetic position of a fossil taxon is impossible to assess without some understanding of the relationships of the Recent taxa. This, it can be suggested, is one of the primary reasons we have had difficulty in evaluating the relationships of many fossil taxa. And this is also reflected in the attitude of considering fossils as inherently primitive or ancestral in morphology (if Recent taxa are mosaics of primitive and derived characters, why not also fossil taxa?). That a knowledge of relationships of Recent taxa is of critical importance is elementary: a fossil is first identified as a bird, then perhaps as a nonpasserine, then as a piciform, then as an "advanced" piciform, and finally as a picid. The extent to which we do not understand the relationships of Recent taxa increases the difficulty of testing alternative hypotheses of relationships involving fossil taxa (see Examples 1, 3, and 4 below).

THE NATURE AND IMPORTANCE OF MONOPHYLETIC GROUPS

The delineation of strictly monophyletic groups (Hennig 1966) represents a central goal of systematics in reconstructing the history of life. The importance of monophyletic groups cannot be overestimated because they alone have reality in that such groups are part of the "genealogical nexus" (M. Ghiselin's term). In recent years it has become fashionable in some circles to speak of "minimal" monophyly or of paraphyletic groups, but such groups are classificatory constructs (artifacts of the mind if you will), have no basis in genealogy, and for this reason are to be avoided.

Strictly monophyletic groups are of special concern to paleontologists beyond their contribution to an obvious understanding of cladistic interrelationships. Their recognition is central to the question of constructing and evaluating hypotheses of ancestry and descent, a subject high in the mind of most paleontologists.

HYPOTHESES ABOUT EVOLUTIONARY TREES

WHAT ARE EVOLUTIONARY TREES?

I will begin by distinguishing the concept of evolutionary trees from that of cladograms. As was noted above, cladograms are hypotheses about the pattern of nested synapomorphy. Cladograms need not necessarily be interpreted as a direct expression of phylogenetic history, although certainly most systematists have a predilection to treat them as such. However, cladograms can be viewed strictly in terms of the analysis of pattern, and it therefore becomes necessary to examine the

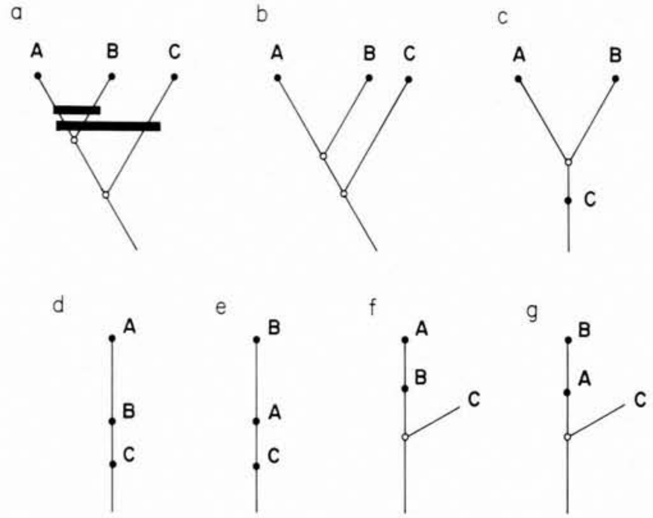

Figure 2. Schematic diagram showing the conceptual difference between a cladogram and an evolutionary tree. In Part a is shown a cladogram of three taxa depicting the nested patterns of synapomorphy (dark rectangles). In the cladogram only *synapomorphic pattern* is implied. In Parts b through g are shown six evolutionary trees, each one of which reflects the pattern of the cladogram. In the tree hypotheses decisions are made whether to postulate speciation events (symbolized by branch points) or directly ancestral taxa (elimination of branch points).

possible evolutionary implications of that pattern. These implications are expressed in terms of evolutionary trees.

Any single cladogram can have a variable number of evolutionary interpretations (Fig. 2). The basic question is to decide whether branch points are to be recognized and a speciation event thus hypothesized, or whether branch points are to be eliminated and an ancestral species specified. Thus, the cladogram of Figure 2a has six possible evolutionary interpretations (Fig. 2b–g). In Figure 2b both branch points are retained and interpreted in terms of speciation events, whereas in Figures 2c–g one or both branch points are eliminated and direct ancestry and descent is specified. Note that all six evolutionary trees are fully consistent with the synapomorphy pattern of the cladogram: in all cases species A and B possess derived characters not shared with species C.

CONSTRUCTING AND TESTING EVOLUTIONARY TREES

In attempting to construct evolutionary trees it is essential that a corroborated species-level cladistic hypothesis is first proposed. In constructing evolutionary trees all ancestral and descendant taxa must be of species rank; terminal taxa may be of any rank. This follows from elementary evolutionary theory: species, not supraspecific taxa, are considered the evolving units of the evolutionary process. The "evolution" of supraspecific taxa is merely the statistical summation of the evolutionary histories of the included species. Thus, genera, families, and so on cannot be designated as ancestral to any other taxon. It has been customary within paleontology to identify supraspecific ancestral taxa, but such a practice almost certainly means (1) the cladistic relationships of the included species are not properly understood, (2) the hypothesis of relationships is imprecisely stated, and/or (3) the supraspecific ancestral taxon is not strictly monophyletic. All of these are to be avoided if the goal is to reconstruct evolutionary history.

Given a cladistic hypothesis (cladogram) for a group of taxa, what might be some of the considerations in evaluating the possible evolutionary trees (see Engelmann and Wiley 1977, and Platnick 1977 for extended discussions)? Ancestors usually have been recognized on two criteria: primitive or intermediate morphology and/or earlier stratigraphic occurrence. Such factors might serve as a basis for postulating ancestor-descendant relationships such as are expressed in Figures 2c–g. How are such hypotheses to be tested?

Consider, for example, the simple hypothesis for Figure 2f in which species B is postulated to be the ancestor of species A. The hypothesis implies that species B is primitive in all features relative to the condition in A. If species B possessed a unique derived character (termed an autapomorphy), we must postulate two evolutionary events to account for its distribution: the evolution of the derived feature in the lineage leading to B and its subsequent loss leading to A. This hypothesis is less parsimonious than one postulating that the autapomorphy evolved after a speciation event producing both A and B (Fig. 2b). On this basis, then, the presence of autapomorphies can be used to reject an ancestor-descendant hypothesis in favor of a hypothesis involving a speciation event.

If we cannot find any autapomorphies in B, does this mean the hypothesis of Figure 2f is to be accepted? Not necessarily, because whereas the hypothesis shown in Figure 2f would appear to be acceptable, so would the hypothesis in Figure 2b. In fact, it does not appear possible to accept an ancestor-descendant hypothesis without at the same time accepting the speciation hypothesis. Indeed, seemingly the only way to reject the latter is to reject the cladogram on which it is based (Platnick 1977). What this means, therefore, is that there are no theoretical grounds for preferring *only* an ancestor-descendant hypothesis.

Stratigraphic data do not help our evaluation of evolutionary trees as much as it might first seem. Although paleontologists often rely heavily on stratigraphic data to specify ancestral taxa, clearly the problem of ancestry and descent is first and foremost a morphological problem. If, as in Figure 2f, we assume taxon B to be primitive morphologically and to occur earlier in the fossil record, then the hypothesis would appear to be highly acceptable. But, how do we reject the hypothesis shown in Figure 2b? Indeed, it would seem we cannot (see Example 5 below). Furthermore, if B occurred later in time than A, could we therefore reject the hypothesis shown in Figure 2f? Yes, but only if (1) we had certain knowledge of the stratigraphic ranges of A and B, and (2) we had certain knowledge that A and B both occurred only within the same stratigraphic sequence and were not geographically distributed elsewhere. But all this seems highly conjectural and would almost certainly call for *ad hoc* assumptions.

Perhaps an important consideration of this discussion should be that paleornithology does not deal with a dense fossil record extending over large periods of time. The theoretical and practical questions posed by such a situation simply do not exist (even in paleomammalogy such occurrences are very rare). If so, then concern with identifying ancestors is perhaps a moot point.

THE FUTURE OF AVIAN PALEONTOLOGY

The future contributions of avian paleontology in deciphering the evolutionary history of birds seem inescapably linked to progress in avian systematics in general. Until we have highly corroborated phylogenetic hypotheses of Recent taxa, our attempts to understand the phylogenetic significances of fossil taxa will be only partially successful (see Examples 1 and 4 below). This is a minority viewpoint within vertebrate paleontology in general, and paleornithology in particular. Traditional opinion holds that only the discovery of more fossil material will ultimately reveal the course of avian phylogeny (Brodkorb 1971:20). I consider this concept to be mistaken for the theoretical reasons presented above.

The purpose of this paper, up to this point, has been to stress the importance of systematic theory in the methodology of avian paleontology. In the final section these theoretical ideas will be given expression in specific examples in order to demonstrate that traditional paleontological analysis has sometimes led to questionable conclusions. The purpose of this section is not to refute the specific conclusions of the examples, but to point out that different theoretical approaches call for alternative hypotheses that generally have not been considered. Thus, the examples were chosen not for their taxonomic interest but solely to illustrate the theoretical points raised in this paper.

SOME EXAMPLES OF PALEORNITHOLOGICAL METHODOLOGY

EXAMPLE 1. The phylogenetic analysis of fossil taxa: the relationships of *Alexornis* (Brodkorb 1976).

Brodkorb (1976) recently described a new species, *Alexornis antecedens,* from the Upper Cretaceous of Baja California. Based on a comparison of six elements, he concludes (1976:70) that:

> The resemblances of *Alexornis* are closest to certain members of the Piciformes and Coraciiformes. Within those two orders the piciform family Bucconidae and the coraciiform family Momotidae have the most similarity to the fossil. The fossil shares certain characters with both Bucconidae and Momotidae, some with Bucconidae alone, and some with Momotidae alone; *but more of its characters are unique* [italics added].

After a tabulation of similarities among *Alexornis,* Momotidae, and the Bucconidae, the hypotheses that *Alexornis* is related to the Coraciiformes, on the one hand, or to the Piciformes, on the other, are rejected. On the basis of a "mixture" of "coraciiform" and "piciform" similarities, Brodkorb concludes (1976:73): "Both morphology and the temporal sequence thus suggest *Alexornis* as the presumptive ancestor of the orders Coraciiformes and Piciformes."

There are two separate questions that need to be discussed when analyzing the phylogenetic position of a fossil taxon such as *Alexornis,* neither of which were considered in this study. First, what are the precise cladistic relationships of the fossil taxon? Second, once the cladistic relationships have been determined, what can we say about the various hypotheses regarding ancestry and descent that might be formulated?

Brodkorb's analysis of phylogenetic relationships was based entirely upon an assessment of overall similarity, and no attempt was made to distinguish between primitive and derived similarities. A second major problem is the attempt to postulate relationships of a fossil taxon in the absence of a corroborated cladistic hypothesis for the Recent taxa. Whereas the Bucconidae are more or less primitive morphologically within the Piciformes (S. Simpson and J. Cracraft, in prep.), the Momotidae are relatively advanced within the Coraciiformes (Cracraft, in prep.; P.J.K. Burton, in prep.; David Maurer, in prep.); thus the use of these two families to characterize the two orders is questionable. Furthermore, the precise interrelationships of coraciiform groups, the piciforms, and the passeriforms are as yet unsettled. Thus, any fossil such as *Alexornis* must be evaluated in light of these observations. It would seem that the phylogenetic position of this fossil is still an open question.

Finally, what about the hypothesis that *Alexornis* is ancestral to both Coraciiformes and Piciformes? Brodkorb himself presents sufficient evidence to reject this hypothesis; his support for it, on the other hand, is derived from two traditional paleontological arguments: apparent "intermediate" morphology and earlier stratigraphic occurrence. But Brodkorb notes that there are a minimum of 20 features "unique" to *Alexornis*. Assuming that these are autapomorphies of *Alexornis,* then if *A. antecedens* is an ancestor, we must postulate at least 20 character reversals. This hypothesis is clearly less parsimonious than assuming *Alexornis* is the sister-taxon of some group and that these features evolved only in the *Alexornis* lineage.

EXAMPLE 2. Character-analysis and the determination of relationships: the case of *Protornis* (Olson 1976).

Olson (1976) recently restudied the lower Oligocene fossil bird, *Protornis glariensis,* a species known from a slab containing limbbones and various other elements found in Switzerland about 140 years ago. He makes a strong case that *Protornis* is related to the Todidae and Momotidae within the Coraciiformes, and then states (p. 115):

> The proportions of the bill and of the hindlimb and toes preclude its assignment to the Todidae. In all of its important features it agrees with the Momotidae. It differs from the modern forms of the family mainly in the shorter mandibular symphysis and the higher, more expanded sternocoracoidal process of the coracoid. *Protornis glariensis* should, therefore, be assigned to the family Momotidae.

Olson concludes (p. 188) from this that ". . . the existence of *Protornis* in the lower Oligocene of Switzerland now provides evidence that the family Momotidae, presently confined to the New World, actually had its origins in the Old World."

Although he may be entirely correct in his phylogenetic assessment and zoogeographic conclusions, Olson's own data and analysis permit an alternative hypothesis. As mentioned, Olson presents evidence that *Protornis,* the Todidae, and the Momotidae shared a common ancestor, and the latter two families have been considered sister-groups within the Coraciiformes by previous workers. An alternative hypothesis to be considered is a sister-group relationship between *Protornis* on the one hand and Todidae + Momotidae on the other. This hypothesis certainly would make more sense zoogeographically by restricting the todid-momotid lineage to the New World. On the basis of the present evidence this hypothesis cannot be rejected for it has not been shown that *Protornis* actually shares one or more derived characters with the Momotidae. It would seem that the absence of a primitive-derived character analysis prevents a more specific statement about the relationships of *Protornis*.

EXAMPLE 3. The logic of evaluating phylogenetic hypotheses: Gingerich (1976) on palaeognath phylogeny.

A number of workers have argued for the monophyly of the ratite birds and tinamous (palaeognaths) by suggesting that some shared characters, including the palaeognathous palate, rhamphothecal structure, and enlarged ilioischiatic fenestra, are derived or unique to these birds (Bock 1963; Parkes and Clark 1966; Cracraft 1974b). Gingerich (1976:31–32) presents two opposing arguments: (1) the three similarities are in fact not derived to the ratites but are primitive, and that therefore (2) "it is possible, even probable, that the groups of living ratites and the tinamous are paraphyletic" (1976:32).

The discussion here is not concerned with the evidence Gingerich raises against the hypotheses about character polarity proposed by previous workers. After all, it is important to examine and criticize such hypotheses. But it is one thing to argue that the hypothesized derived characters of a group are primitive and quite another to conclude that the group is not therefore monophyletic. The second argument does not follow necessarily from the first and to link them confuses two separate aspects of phylogenetic analysis: on the one hand, the acceptance of a hypothesis of synapomorphy and its use in defining monophyletic groups, and on the other, the preference of one phylogenetic hypothesis over another.

If the three shared similarities discussed by Gingerich are primitive, then he is correct in stating that evidence for ratite-tinamou monophyly remains to be discovered. Nevertheless, this does not mean we must reject that hypothesis of monophyly, because preference for, or rejection of, any particular phylogenetic hypothesis is dependent upon its status relative to alternative hypotheses. Thus, without undermining the importance of an evaluation of character polarity, the ultimate criticism of a phylogenetic hypothesis is the presentation of evidence that one or more of the taxa are more closely related to other taxa of birds: in effect to argue preference for an alternative hypothesis based on shared derived characters. As far as the tinamous or ratite taxa are concerned, no alternative hypotheses were proposed by Gingerich nor are any given strong support in the literature.

This bring us back to a consideration of the three observed similarities said by Gingerich to be primitive. If they are primitive within tinamous and ratites, this implies they are synapomorphous (derived) at some higher taxonomic level, perhaps to birds as a whole or to birds + some reptilian taxon. Indeed, Gingerich attempts to suggest this, but an identification of the taxonomic level is not made explicit (in fact, no argument is presented against the peculiar rhamphotheca being derived). Nor was it suggested that the large number of postulated derived characters interrelating the ratites themselves (Cracraft 1974b) are also primitive or convergent, which logically would be the case if the ratites are not related to one another.

Thus, Gingerich's criticism of palaeognath monophyly, while well-intentioned with respect to examining the validity of some of the postulated polarity sequences, is theoretically in error with regard to using those sequences to evaluate alternative phylogenetic hypotheses.

EXAMPLE 4. The analysis of "intermediate" fossils: the case of *Presbyornis* (Feduccia 1976, 1977, 1978).

The search for "missing links" has been a relentless preoccupation of paleontology for over a century. Darwin (1859:280) set the tone for paleontological methodology: "I have found it difficult, when looking at any two species, to avoid picturing to myself, forms *directly* intermediate between them" [italics in original]. So it has been that paleontologists have sought to find fossil intermediates between Recent taxa, for it is commonly thought that only by such discoveries can the distant connections of phylogenetic history be discerned. However, Darwin saw a problem to the search for intermediates between Recent taxa, and he followed the above statement with the observation: "But this is a wholly false view; we should always look for forms intermediate between each species and a common but unknown progenitor. . . ."

Despite Darwin's exhortation, the temptation to seek intermediate fossils has remained high, and has found some expression in several recent studies of fossil birds. Perhaps the most publicized such fossil is *Presbyornis,* a genus containing several species known from the Eocene of western North America and possibly the Eocene of South America. The importance of this fossil is stated explicitly by Feduccia (1978:300):

> Although almost all the vertebrate groups are replete with so-called 'missing links' that have added greatly in elucidating their phylogenies, *Presbyornis* represents the first known avian fossil to form a link between a number of major living orders of birds. *Presbyornis* is an evolutionary mosaic, combining a strange montage of morphological characteristics of shorebirds, modern ducks and allies, and modern flamingos.

The arguments and empirical support for regarding *Presbyornis* to be intermediate between shorebirds, ducks, and flamingos are extremely complex. In essence, *Presbyornis* is said to have a cranium very similar to that of a duck and the postcranial skeleton of a recurvirostrid shorebird and flamingo. Postcranial material of *Presbyornis* is abundant and associated in the same matrix, but little, if any, of it is directly articulated. Consequently, an incontrovertible argument for the conspecificity of the cranial and postcranial material has not been presented at this time.

It is not the purpose of this example to discuss the morphological evidence relating to Feduccia's claim of intermediacy. Rather, I wish to cite some difficulties with his argumentation that illustrate potential problems in the phylogenetic analysis of fossils, in particular the interpretation that certain fossils may be intermediate in character.

The major problem presented by the example of *Presbyornis* is our lack of understanding of the phylogenetic relationships among Recent taxa. Nevertheless, our present conceptions about these interrelationships define an array of hypotheses not considered by Feduccia. Three major criticisms can be made.

First, Feduccia implies (1976:600) that recurvirostrids (avocets, stilts) are the sister-group of other "shorebirds," but this is almost certainly not true; moreover, non-shorebird charadriiforms are excluded from his argument. Recurvirostrids have often been thought to be among the more advanced charadriiforms, and certainly their skeletal anatomy has not been considered primitive within the order. If so, this creates a devastating difficulty for Feduccia's hypothesis, because the argument for intermediacy depends upon showing that the similarities of *Presbyornis* and charadriiforms are primitive, not advanced. Thus, the acceptance of at least the outlines of a phylogeny of the Charadriiformes becomes essential, and what we think is understood about that is not favorable to Feduccia's hypothesis. Virtually all previous workers, for example, Lowe (1923) and Stresemann (1927–34), have believed the shorebirds (i.e., recurvirostrids, scolopacids, charadriids) to be among the more advanced charadriiforms.

Second, Feduccia's argument in support of a link between *Presbyornis* and flamingos borders on the circular in that some of his conclusions seem imbedded or implied in his premises. The conclusion of interest here is that flamingos are not at all closely related to ciconiiform birds, as has been thought by many previous workers. He argues that *Presbyornis* is similar to flamingos and recurvirostrids but not to ciconiiforms. His unstated premise is that because there is no perceived similarity between *Presbyornis* and ciconiiforms, the latter cannot have a relationship to flamingos. *Presbyornis* essentially becomes the arbiter of relationships among these Recent taxa before the relationships of the fossil are fully assessed. Any argument for intermediacy must treat the problem of a ciconiiform-flamingo relationship more rigorously, principally by showing that ciconiiforms are more closely related to some other taxon.

Third, the hypothesis of a link between *Presbyornis* and anatids is weakened, it would appear, by Feduccia's exclusion from his argument of the anseriform family Anhimidae and of the order Galliformes. Few, if any, modern workers have seriously doubted a sister-group relationship between anatids and anhimids. The latter family is generally considered to be primitive in most of its features relative to the anatids, particularly in cranial characteristics. The purported skull of *Presbyornis* is compared to an *advanced* condition within the anseriforms and not one that is primitive, a line of argumentation counter to the concept of intermediacy. Furthermore, many previous systematists such as Beddard (1898), Simonetta (1963), and Prager and Wilson (1976) have called attention to a possible close relationship of the anseriforms and galliforms. Thus, any argument for a link between *Presbyornis* and anatids must also be presented in the context of an analysis of these previous hypotheses.

The point of this example is to indicate the complexity of arguments that are involved with any hypothesis linking Recent taxa with fossils. Most of this complexity, if not all of it, relates to evaluating the interrelationships of Recent taxa before assessing the phylogenetic affinities of fossils. If fossil taxa are to have significance as intermediate links, then they must share some of the primitive features of the taxa being linked. This does not seem to be the case with *Presbyornis,* and given present evidence it is difficult to assign the material of *Presbyornis* to the charadriiforms, Anatidae, or the Phoenicopteridae. Certainly, the assertion that *Presbyornis* is an important link between modern groups of birds is in need of reevaluation.

EXAMPLE 5. The identification of ancestors: the case of *Limnofregata azygosternon* (Olson 1977).

In an excellent descriptive systematic paper Olson (1977) described a nearly complete skeleton of a frigatebird-like species from the early Eocene of Wyoming. The species is similar to frigatebirds in many respects but also shares some features with *Phaethon* and *Sula.* Following a detailed comparative analysis Olson concluded (1977:31):

> There is nothing that I can detect in the skeleton of *Limnofregata* that precludes its being directly ancestral to *Fregata.* The fact that by the early Eocene it was already markedly specialized along much the same lines as the modern genus renders this possibility plausible.

Olson's argument for a direct ancestry by *L. azygosternon* is one of the better examples of such a claim to be found in the paleornithological literature. He specifically points out that most of the features shared between *L. azygosternon* and other pelecaniforms are probably primitive, whereas those shared with *Fregata* seem derived solely to that lineage. Whether *L. azygosternon* has any unique features all its own is uncertain, but Olson seems not to have found any for none are specifically mentioned.

The hypothesis that *L. azygosternon* is the direct ancestor of the modern genus *Fregata* would not seem to be capable of rejection based on any evidence presented by Olson. On the other hand, for the theoretical reasons presented above, neither can the hypothesis that *L. azygosternon* and *Fregata* share a sister-group relationship be rejected. It is just as "plausible" as the hypothesis of direct ancestry, and reasons are not presented by Olson for preferring the latter. In this case Olson's decision to invoke direct ancestry is not significantly misleading because the relationship between the fossil and Recent taxa seems to be properly analyzed.

CONCLUSIONS

Very little attention has been paid within avian paleontology to problems of systematic theory and methodology. The practices of avian paleontologists are frequently empirical in approach and are governed by assumptions that fossils are intrinsically important in matters of phylogenetic inference, character phylogeny, or the analysis of intermediate taxa.

However, an alternative perspective is possible, one that does not eliminate the importance of fossil taxa but integrates them into a testable method of phylogenetic inference focused primarily on Recent taxa. This alternative is cladistic analysis (phylogenetic systematics). Monophyletic groups, whether fossil, Recent, or a mixture of both, are defined in terms of shared derived characters (synapomorphy). From an analysis of nested synapomorphy patterns, cladistic hypotheses (cladograms) are formulated. These hypotheses in turn can be used to evaluate hypotheses about evolutionary history (trees).

It can be shown that the application of cladistic theory to paleontological practice increases the precision of phylogenetic research. This precision is manifested particularly in discussions about the phylogenetic relationships of fossil and Recent taxa, the analysis of morphologically intermediate fossil taxa, and the postulation of ancestral species level taxa.

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THE ARCHAEOTROGONIDAE OF THE EOCENE AND OLIGOCENE PHOSPHORITES DU QUERCY (FRANCE)[1]

By Cécile Mourer-Chauviré[2]

ABSTRACT: The genus *Archaeotrogon* Milne-Edwards was described in the last century from the fossiliferous deposits of "Phosphorites du Quercy." New excavations carried out at these sites have resulted in additional avian specimens that we have been able to assign to the three previously described species of *Archaeotrogon*. The temporal distribution of these species is discussed, and a new species is described.

The species of *Archaeotrogon* do not have the heterodactyl structure of the foot characteristic of modern trogons, although this structure had already been acquired in some contemporaneous forms. It appears that archaeotrogons constituted a distinct family, the Archaeotrogonidae, that evolved parallel with the family Trogonidae, or true trogons.

RESUME: Le genre *Archaeotrogon* Milne-Edwards a été décrit au siècle dernier dans les gisements des Phosphorites du Quercy. De nouvelles fouilles effectuées dans ces gisements ont permis de retrouver les trois espèces précédemment signalées et de leur attribuer un certain nombre d'éléments du squelette. Leur position chronologique a pu être précisée et une nouvelle espèce a été décrite.

Les *Archaeotrogon* ne présentent pas la structure du pied hétérodactyle caractéristique des trogons actuels bien que cette structure soit déjà acquise chez des formes fossiles du même âge. On peut donc penser que les *Archaeotrogon* constituent une famille différente ayant évolué parallèlement à celle des Trogonidae ou vrais trogons.

The "Phosphorites du Quercy" are deposits that filled sinkholes in the karst topography of the departments of Tarn-et-Garonne, Lot, and Aveyron, to the southwest of the central French massif. These deposits were very actively exploited for the extraction of calcium phosphate between approximately 1870 and 1880. During the course of mining, many specimens of fossil vertebrates, as well as molluscs and insects, were discovered in these localized deposits. The first discoveries of bird bones were announced by Lydekker (1891), followed by Milne-Edwards (1892). The birds of the Phosphorites du Quercy were thereafter the subject of an important work by Gaillard (1908). But the bones of the early collections did not bear precise data as to which sinkhole they were collected from, and the phosphorite deposits at Quercy include faunas that extend from the Upper Bartonian (Robiac's mammal zone) all the way to the Upper Stampian (Boningen's mammal zone).

New work was undertaken at Quercy by the group RCP 311 (Recherche cooperative sur programme 311) of the CNRS (Centre national de la Recherche scientifique), composed of researchers from the universities of Montpellier, Paris VI, and Lyon I. In the course of this recent work, the beds were excavated separately and each was well dated by means of its mammalian fauna (Crochet et al. 1972; de Bonis et al. 1973; Hartenberger 1973; Cavaillé et al. 1974; Hartenberger et al. 1974; Sigé 1974, 1976; Vianey-Liaud 1976; Sudre 1977; Crochet 1978).

I had undertaken the revision of the avifaunas of Quercy, and for that reason I was able to collect together the older documents kept in the collections of the National Museum of Natural History in Paris, the Natural History Museum and the Department of Earth Sciences of Lyon, and the University of Utrecht, as well as the newer documents amassed by the researchers of the University of Montpellier and the University of Paris VI.

The living trogons belong to a single family, the Trogonidae, a group of eight genera. Five of these live in Central America, South America, and the Antilles; two in tropical Africa, and one in southeast Asia (Peters 1945); see Figure 1. Trogons appear to have been a constant element of the paleoavifauna of Europe, ever since they were first described by Milne-Edwards (1867–1871) from the lower Miocene (Aquitanian) deposits of the department of Allier under the name of *Trogon gallicus*. (The generic name of this fossil form was later changed to *Paratrogon* by Lambrecht (1933).) Milne-Edwards (1892) subsequently discovered the presence of trogons in the Phosphorites du Quercy and created for these forms the genus *Archaeotrogon*. The new excavations at Quercy have shown that the trogons are often the most abundant elements in the avifauna, particularly in those beds that date from the upper Oligocene, such as Pech Desse, and above all, Pech du Fraysse. Futhermore, Olson (1976) has shown that one of the

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birds found in the "Glarner Fischschiefer" in Switzerland (see Fig. 1), and known as *Protornis glaronensis* von Meyer 1884, possessed the heterodactyl foot structure characteristic of the living trogons. Therefore, that specimen should be considered to be a member of the Trogonidae, even though the holotype of the species should be placed among the Momotidae; Peyer (1957) believed this species to be a member of the Alcedinidae. The age of the "Glarner Fischschiefer" is believed to be lower Oligocene (Sannoisian) because of the fish fossils found there. In addition to extinct forms of the European Tertiary, two living species of trogonids have been found as fossils in Pleistocene deposits: *Trogon surrucura* Vieillot in Brazil and *Temnotrogon roseigaster* (Vieillot) in the Dominican Republic (Brodkorb 1971).

SYSTEMATICS

Order Alcediniformes Feduccia 1977

Superfamily Trogonoidea Feduccia 1977

Archaeotrogonidae new family

TYPE GENUS: *Archaeotrogon* Milne-Edwards 1892

DIAGNOSIS: Trogons, that differ from all species of the family Trogonidae by lacking the heterodactyl foot characteristic of that family.

TEMPORAL AND GEOGRAPHIC DISTRIBUTION: Upper Eocene to lower Oligocene. Phosphorites du Quercy, France.

REMARKS: The family Archaeotrogonidae contains only the type genus. Although the archaeotrogons were characterized by the primitive structure of their tarsometatarsus, i.e., the lack of heterodactyly, in deposits of the same age as those at Quercy there existed a trogon whose foot already had a heterodactyl structure. One may therefore consider the forms of Quercy as a line parallel to that of the true trogons, which belong to the family Trogonidae. The Trogonidae contains the fossil bird from the Glarner Fischschiefer (Olson 1976), the extinct genus *Paratrogon,* as well as the living genera (*Pharomachrus, Euptilotis, Priotelus, Temnotrogon, Trogon, Apaloderma, Heterotrogon,* and *Harpactes*).

Genus *Archaeotrogon* Milne-Edwards 1892

TYPE SPECIES: *Archaeotrogon venustus* Milne-Edwards 1892

DESCRIPTION: *Archaeotrogon* has been described primarily on the basis of its humerus, and humeri are very abundant in the older collections. In addition to the humeri, Lydekker (1891) referred some coracoids (not figured) and Milne-Edwards (1892) some carpometacarpi (not figured) to the genus. Gaillard (1908) described and figured a tarsometatarsus that he attributed to the species *A. cayluxensis*. In certain sites at Quercy, specimens of *Archaeotrogon* are very numerous and represent more than half of the bird bones found in these beds. It is logical to assume that, if the most common humerus belongs to the genus *Archaeotrogon,* then the most common ulna, the most common carpometacarpus, the most common coracoid, etc., should likewise belong to that genus. I have therefore attributed to that genus a certain number of skeletal elements collected from all the sites where the humerus of *Archaeotrogon* was found, but it is also true that these elements show analogies with the corresponding bones of living trogons. I must point out that I have never found articulated bones in the Phosphorites du Quercy. This is probably due in part to the way the fossiliferous cavities were filled, and is partly a result of the methods of excavation, which included washing and screening techniques. There cannot, therefore, be an absolute certainty that the bones attributed to *Archaeotrogon* truly belong to that genus, but there is a strong probability that they do.

COMPARISON WITH LIVING TROGONIDAE. At the Natural History Museum of Leiden I was able to study skeletons belonging to the genera *Harpactes, Trogon, Pharomachrus,* and *Prioteles*. The genus *Archaeotrogon,* when compared with the Trogonidae, shows the following similarities and differences (characters of the Trogonidae in parentheses).

Humerus. Similarities: (1) same general form; (2) head enlarged and flattened; (3) internal trochanter very prominent; (4) tricipital fossa large; (5) pectoral crest lengthened; (6) distal extremity transversely widened; (7) tricipital grooves forming a large depression.

Differences: (1) proximal end very wide transversely (proximal end less wide transversely); (2) head rather flattened (head more swollen); (3) internal trochanter more strongly bent backwards and downwards; (4) no pneumatic orifice in the sub-trochanteric fossa (pneumatic orifices in the sub-trochanteric fossa); (5) tricipital fossa larger; (6) ligamental groove very long (ligamental groove rather short); (7) section of shaft flattened (corresponding section of shaft more circular); (8) impression of M. brachialis anticus long and shallow (impression of M. brachialis anticus more circular and sharply marked); (9) radial condyle rather long and narrow in the center (radial condyle much more rounded); (10) epitrochlea and epitrochlear prominence little developed (epitrochlea and epitrochlear prominence more developed and prominent on the internal side); (11) tricipital grooves very large and deep (tricipital grooves wide but not very deep); (12) external tricipital groove sharply marked and bordered by two raised crests (external tricipital groove less marked); (13) epicondyle well developed (epicondyle not very developed).

Ulna. Similarities: (1) general shape very similar; (2) same positioning of internal and external glenoid facets; (3) prominence for anterior articular ligament well marked; (4) shaft circular; (5) same general shape of distal end.

Differences: (1) proportionately shorter and more curved (longer and less curved); (2) glenoid surfaces oriented obliquely to long axis of bone (glenoid surfaces oriented almost parallel to long axis of bone).

Radius. Differences: (1) general form rectilinear (general form curved at distal end); (2) distal end spatulate, practically symmetrical to long axis of bone (distal end assymmetric).

Carpometacarpus. Similarity: Short and wide in both groups.

Differences: (1) radial apophysis forms a spur comparable to that seen in *Hoplopterus spinosus,* the Spurwing Plover; this radial apophysis was noted by Milne-Edwards (1892) (no spur in the genera *Harpactes, Trogon, Pharomachrus,* and *Prioteles*); (2) metacarpal III lies almost parallel to metacarpal II (metacarpal II at a very oblique angle to metacarpal III; the gap between the metacarpals is very wide at the distal end, and the distal end is very wide); (3) internal digital facet lies in the same plane as the external digital facet (internal digital facet lies at a different level than external digital facet).

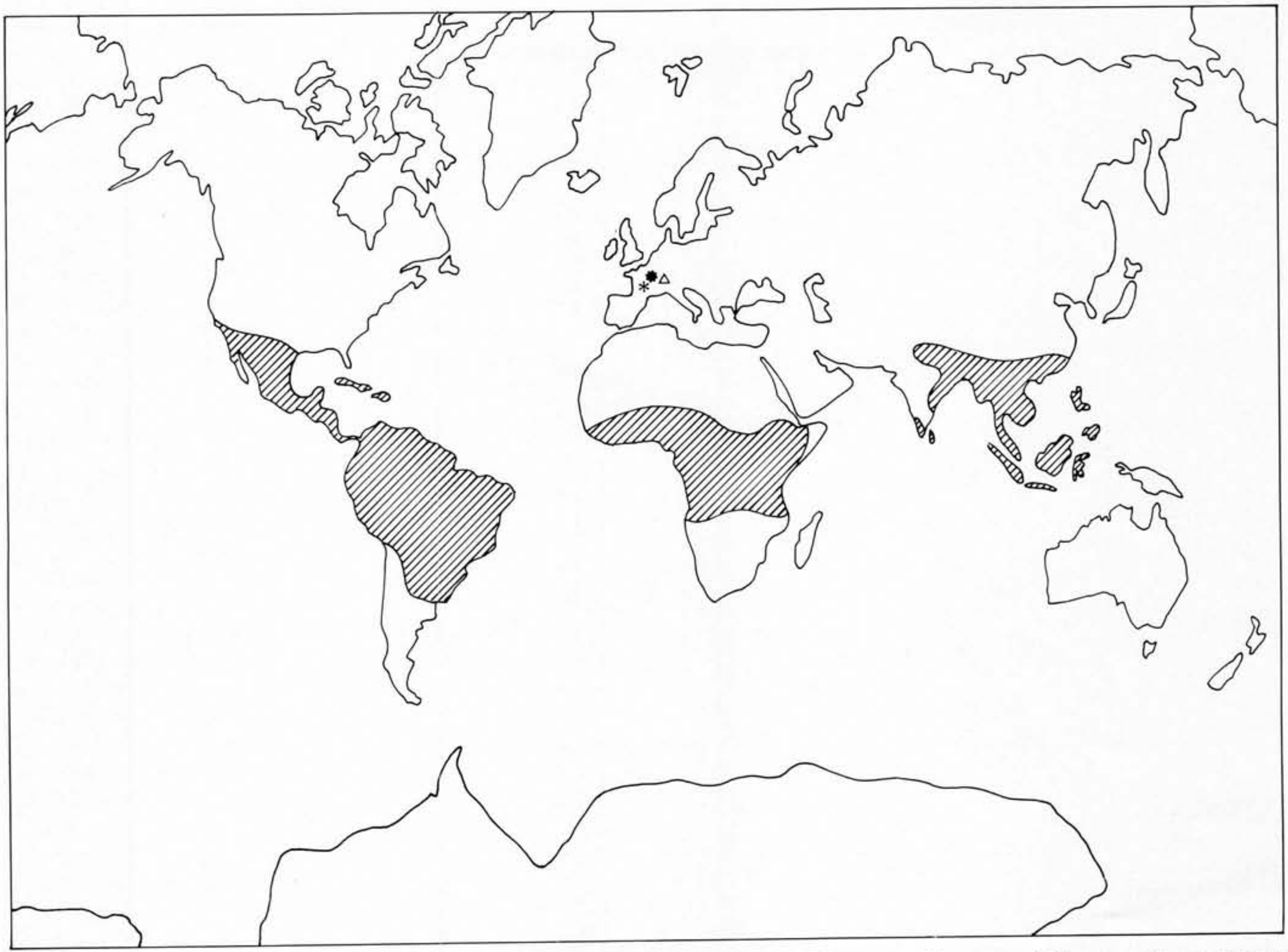

Figure 1. Geographic distribution of living trogons (hatching) and fossil trogons: (*) *Archaeotrogon,* Eocene and Oligocene, Phosphorites du Quercy, France; (●) *Paratrogon,* Miocene of l'Allier, France; △ Trogonidae, Oligocene, Glarner Fischschiefer, Switzerland.

Coracoid. Similarities: (1) same general shape of the head, glenoid facet, and scapular facet; (2) no sub-clavicular foramen; (3) distal end large and paddle-shaped; (4) sternal facet almost perpendicular to the long axis of the bone.

Differences: (1) proportionately slightly shorter and more massive (proportionately longer and more slender); (2) sub-clavicular apophysis usually broken at the extremity, but rather wide at its origin (sub-clavicular apophysis narrow); (3) sternal facet short and strongly curved (sternal facet longer and not very curved); (4) hyosternal apophysis weakly developed on the external side and barely present on the internal side (hyosternal apophysis very well developed both externally and internally); (5) strongly marked groove for the ligament of the sterno-coracoidal muscle on the upper surface of the bone (very shallow groove for the sterno-coracoidal muscle).

Femur. Similarity: General shape very similar.

Differences: (1) proximal end rather flattened (proximal end more swollen); (2) no pneumatic orifice under the trochanter (pneumatic orifice present in the genus *Trogon,* but not in *Harpactes*); (3) fossa present below the articulation on the posterior side (no fossa present below the articulation on the posterior side); (4) shaft slender (shaft heavy in the genus *Trogon*, but slender in *Harpactes*); (5) distal end flattened (distal end more swollen).

Tibiotarsus. Similarities: (1) relatively short in both groups; (2) proximal articulation perpendicular to the long axis of the bone; (3) tibial crests poorly developed; (4) supratendinal bridge lies on the internal side of the bone; (5) shallow groove for the extensor muscle of the digits.

Differences: (1) shaft relatively slender and slightly widened toward the distal end (shaft heavier and widens toward the distal end); (2) external rugosity of oblique ligament well developed (external rugosity of oblique ligament poorly developed).

Tarsometatarsus. Similarity: Same general proportions as compared to the femur and tibiotarsus.

Differences: (1) internal trochlea turned slightly backward; digit I points backwards, digits II, III, and IV forwards (internal trochlea turned completely toward the rear; digits I and II point backwards, digits III and IV forwards); (2) hypotarsus with a channel pointing externally between two subequal calcaneal ridges (hypotarsus with a very strong median ridge (ridge 1) and two canals situated externally to that median ridge (see Fig. 2); (3) two very evident superior foramina, the

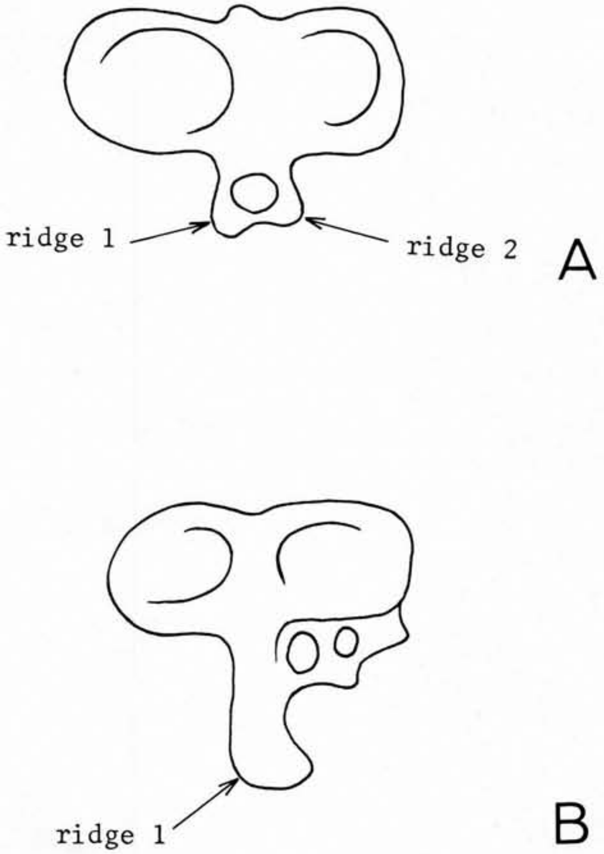

Figure 2. Diagram showing the position of the calcaneal ridges of the hypotarsus in the genus *Archaeotrogon* (A) and in the living genus *Trogon* (B). Right tarsometatarsus, proximal views.

internal foramen larger than the external foramen (two hardly noticeable superior foramina of equal size); (4) inferior foramen wide and in a deep groove, foramen lies clearly proximal to the trochleae (inferior foramen very small and in a shallow groove; foramen very close to trochleae); (5) shaft flattened anteroposteriorly (shaft rather flattened mediolaterally); (6) internal cotyla prominent and sharply defined (internal cotyla weak); (7) metatarsal facet well marked (metatarsal facet poorly marked).

It is the tarsometatarsus that shows the greatest contrast between the Archaeotrogonidae and the Trogonidae. *Archaeotrogon* does not have the heterodactyl foot characteristic of the living trogons and unique among all the birds.

COMPARISON WITH THE GENUS *Paratrogon* LAMBRECHT 1933. This genus contains the single species *Paratrogon gallicus* Milne-Edwards 1871, described from the Aquitanian deposits of Allier, and is known only from two humeri (Milne-Edwards 1867–1871:395–396, pl. 177, figs. 18–22).

The genus *Archaeotrogon* is noticeably different from *Paratrogon,* and contrary to the opinion of Lambrecht (1933), I believe that *Paratrogon* is closer to the living trogons than to *Archaeotrogon* and should therefore be placed in the family Trogonidae. When comparing the humerus of *Archaeotrogon* to that of *Paratrogon* one finds almost the same differences as noted between the humeri of *Archaeotrogon* and the living Trogonidae. The characters of the humerus are shown in Table 1.

COMPARISON WITH THE CORACIIFORMES AND THE CAPRIMULGIFORMES. Feduccia (1977) has shown that the shape of the stapes, the middle ear ossicle in birds, can be used to show phylogenetic relationships. The trogonid stapes has a bulbous and hollow basal part with a large orifice on the posterior side, and a stapedial process arising from the edge of the basal part. This morphology is very different from the primitive morphology of the stapes, which is that of a flat discoidal plate with the stapedial process arising from its center. The trogon morphology of the stapes is found in four avian families previously assigned to the order Coraciiformes: Meropidae (bee-eaters), Alcedinidae (kingfishers), Momotidae (motmots), and Todidae (todys). According to Feduccia (1977:21), this similarity "argues strongly for monophyly of the trogons and bee-eaters/kingfisher/motmot/tody assemblage." The earlier classification has therefore been modified, and the four families mentioned above have been removed from the Coraciiformes and joined with the Trogonidae in the new order Alcediniformes. It would be interesting to know if the osteology of the primitive trogonids can support this relationship.

I was unable to compare *Archaeotrogon* with the Momotidae or the Todidae, which are restricted to the tropical zones of Central America and the Antilles, but I did make the comparison with the Meropidae and the Alcedinidae. There are similarities in the bones of the hindlimb of the latter two families and those of *Archaeotrogon,* but there are very great differences in the shape of the humerus.

In *Merops,* the proximal end of the humerus is not transversely widened, there is no tricipital fossa, the internal trochanter is low, the pectoral crest is short, the distal end is not very wide transversely and sits obliquely to the long axis of the shaft, the epitrochlea is very prominent toward the base, and the tricipital grooves do not occupy a deep and wide depression.

In the genera *Alcedo* and *Dacelo,* the head of the humerus is globular, the internal trochanter weakly developed, the subtrochanteric fossa very small, the pectoral crest very short, and the distal end is very different from that of *Archaeotrogon*.

On the other hand, there is a certain similarity between the humeri of *Archaeotrogon* and the living Caprimulgiformes (*Caprimulgus* and *Chordeiles*). This resemblance is particularly strong in the new species of *Archaeotrogon,* which has a crest obliquely crossing the tricipital fossa (see Figs. 4t–w, 10) as in the genus *Caprimulgus*. There are likewise other characters in common in both the humerus and other bones of the skeleton. The ancestral forms of the Caprimulgiformes are unknown, since the Aegialornithidae of the Eocene and Oligocene that have previously been placed in this order (Brodkorb 1971; Collins 1976) should actually belong to the Apodiformes (Harrison 1975; Mourer-Chauviré 1978). One may therefore speculate as to the possibility of *Archaeotrogon* being related to the Caprimulgiformes.

Archaeotrogon venustus Milne-Edwards 1892

Figure 3

1891 Genus b Lydekker, p. 78, fig. 3
1892 *Archaeotrogon venustus* Milne-Edwards, p. 5–7
1908 *Archaeotrogon venustus* Milne-Edwards, Gaillard, p. 66–67, fig. 14, pl. 3, figs. 20–23

Table 1. Morphological characters of the humerus of *Archaeotrogon, Paratrogon,* and the living Trogonidae.

Characters of the Humerus	*Archaeotrogon*	*Paratrogon*	Living Trogons
Proximal end	Very large and very recurved medially	Not large, slightly recurved medially	Not large, slightly recurved medially
Tricipital fossa	Large and usually shallow	Narrower	Narrower
Bicipital surface	Very wide transversely	Less wide transversely	Less wide transversely
Ligamental groove	Very long	Not very long	Not very long
Head of humerus	Rather flattened	More swollen	More swollen
Sub-trochanteric fossa	Without pneumatic orifices	Apparently without pneumatic orifices	Pneumatic orifices present
Impression of M. brachialis anticus	Long and shallow	More circular and deep	More circular and deep
Radial condyle	Lengthened and narrowed in the center	More globular	More globular
Epitrochlea	Poorly developed	Strongly developed	Strongly developed
Olecranal fossa	Very deep	Apparently rather deep	Rather shallow
Tricipital groove	Well marked externally and bordered by two prominent ridges	Weakly marked externally	Weakly marked externally and bordered by a ridge

1933 *Archaeotrogon venustus* Milne-Edwards, Lambrecht, p. 625
1971 *Archaeotrogon venustus* Milne-Edwards, Brodkorb, p. 247
1971 *Archaeotrogon venustus* Milne-Edwards, Crochet, p. 316

MATERIAL: Early collections without provenance: complete left humeri, QU 15797, QU 15799, QU 15805; incomplete left humeri, QU 15802, QU 15785; complete right humeri, QU 15781, QU 15782; incomplete right humerus, QU 15804; incomplete left carpometacarpi, QU 15917, QU 15939; complete right carpometacarpus, QU 15882; incomplete right carpometacarpi, QU 15915, QU 15918, QU 15940 (Museum of Paris). Incomplete right humerus, PQ 987; incomplete left humerus, PQ 991 (Museum of Lyon). Two left humeri and one right humerus almost complete (Department of Earth Sciences, Lyon).

Deposits of Pech du Fraysse: left humeri more or less complete, PFR 577, 578, 11034, 11147, 11186; proximal left humeri, PFR 11018, 11031, 11142, 11164, 11112, 11196; distal left humeri, PFR 580, 5105, 5109, 11040, 11188, 11187, 11055, 11056, 11123, 11155, 11062, 11160, 11201, 11116, 11117, 11229, 11230, 11231; shafts of left humeri, PFR 11042, 11191, 11093; right humeri more or less complete, PFR 5106, 5108, 11022, 11195; proximal right humeri, PFR 581, 9545, 11070, 11071, 11080, 11081, 11102, 11121, 11180, 11232, 11233, 11234; distal right humeri, PFR 579, 582, 583, 5107, 7218, 9802, 11029, 11033, 11045, 11046, 11051, 11061, 11066, 11080, 11108, 11149, 11150, 11157, 11189, 11190, 11191, 11192, 11194, 11197; shaft of right humerus, PFR 11063; left coracoids more or less complete, PFR 5112, 5113, 8583, 11058, 11083, 11084, 11085, 11100, 11109, 11124, 11161, 11235; proximal left coracoids, PFR 585, 7050, 11129, 11236; distal left coracoids, PFR 11237, 11238; right coracoids more or less complete, PFR 5111, 11076, 11088, 11095, 11133, 11162, 11166, 11168, 11172, 11205; proximal right coracoids, PFR 584, 8359, 11239; distal right coracoids, PFR 7465, 11126, 11174, 11251, 11240, 11241; left ulnae more or less complete, PFR 3998, 11047; proximal left ulnae, PFR 11098, 11111, 11125, 11204; distal left ulnae, PFR 5118, 9409, 11075, 11130, 11200, 11213; right ulnae more or less complete, PFR 11043, 11136, 11151; proximal right ulnae, PFR 8358, 11110, 11114, 11169, 11198, 11212; distal right ulnae, PFR 593, 594, 3999, 8360, 11068, 11170, 11208, 11242; left carpometacarpi more or less complete, PFR 576, 5110, 11073, 11074, 11167, 11216; proximal left carpometacarpi, PFR 7560, 11243, 11244, 11245, 11246, 11247; distal left carpometacarpi, PFR 586, 587, 7222, 11248, 11249; right carpometacarpi more or less complete, PFR 574, 575, 9546, 11086, 11089, 11090, 11115; proximal right carpometacarpi, PFR 11099, 11127, 11128, 11202, 11250, 11251, 11252; distal right carpometacarpi, PFR 11105, 11253; proximal scapulae, PFR 11103, 11254, 11255, 11256, 11257; distal radii, PFR 11258, 11259, 11260, 11261, 11262, 11263; left femora more or less complete, PFR 11082, 11105; proximal left femur, PFR 11107; distal left femur, PFR 11264; right femora more or less complete, PFR 11060, 11113; proximal right femur, PFR 11265; distal right femora, PFR 11211, 11214, 11266; proximal left tibiotarsus, PFR 11131; distal left tibiotarsus, PFR 11267; almost complete right tibiotarsus, PFR 11203; distal right tibiotarsi, PFR 11096, 11132, 11268; almost complete left tarsometatarsi, PFR 11091, 11175, 11269; distal left tarsometatarsi, PFR 11270, 11271, 11272, 11273; distal right tarsometatarsi, PFR 11274, 11275, 11276, 11277 (Museum of Paris).

Deposits of Escamps A: proximal scapula.

Deposits of Itardies: distal left humerus ITD 548; distal right humeri, ITD 569, 617; proximal right coracoids, ITD 542, 573, 704, 709; distal right coracoid, ITD 691; proximal left ulnae, ITD 678, 684; proximal right ulna, ITD 538; distal right


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ulna, ITD 673; proximal left carpometacarpi, ITD 696, 710; distal left carpometacarpus, ITD 541; proximal right carpometacarpus, ITD 575.

Deposits of Mas de Got B: complete right carpometacarpus, MGB 1545; distal right femur, MGB 1558.

Deposits of Mounayne: proximal right carpometacarpus, MOU 1.

Deposits of Pech Desse: complete left humeri, PDS 1226, 1236; distal left humeri, PDS 1218, 1227, 1234; almost complete right humerus, PDS 1212; proximal right humerus, PDS 1257; distal right humeri, PDS 1223, 1232, 1274; almost complete left coracoids, PDS 1230, 1237; proximal left coracoid, PDS 1243; complete right coracoid, PDS 1244; proximal right coracoid, PDS 1275; distal right coracoid, PDS 1242; proximal left ulna, PDS 1235; distal left ulnae, PDS 1249, 1252, 1269, 1270; distal right ulnae, PDS 1241, 1260; distal right carpometacarpus, PDS 1264; proximal scapulae, PDS 1271, 1278, 1281, 1289; almost complete left femur, PDS 1277; distal right femur, PDS 1280; distal left tarsometatarsus, PDS 1273.

Deposits of Perrière: distal left ulnae, PRR 2599, 2609; proximal left carpometacarpus, PRR 2608; proximal left femur, PRR 2607.

Deposits of La Plante 2: distal left humerus, PLA 1047; shaft of right humerus, PLA 1062; proximal right coracoid, PLA 1071; distal right coracoid, PLA 1066; proximal right ulna, PLA 1065; distal right ulna, PLA 1063; complete right carpometacarpus, PLA 1064; proximal left carpometacarpus, PLA 1073; proximal right carpometacarpus, PLA 1070; proximal scapula, PLA 1069; wing phalanx?, PLA 1067.

Deposits of Roqueprune 2: complete left coracoid, ROQ 310; distal right coracoid ROQ 317; proximal left ulna, ROQ 315; distal right ulna, ROQ 312; distal left femur, ROQ 313; proximal right femur, ROQ 311; proximal scapula, ROQ 318 (University of Montpellier and Paris VI).

Deposits of Boussac 1: almost complete left carpometacarpus.

Deposits of Boussac 2: distal right ulna and distal left ulna.

Deposits of Escamps 3: distal right humerus.

Deposits of Fonbonne 1: proximal left coracoid.

Deposits of Garrigues: proximal right carpometacarpus (University of Utrecht).

DESCRIPTION: *Archaeotrogon venustus* is the smallest species in the genus. It is also the species most abundantly represented in the recently collected material and the best known in regards to the skeleton. All the characters previously indicated in the description of the genus *Archaeotrogon* apply to this species.

MEASUREMENTS: For measurements of this species see Table 2.

Archaeotrogon zitteli Gaillard 1908

Figure 4a–j

1908 *Archaeotrogon zitteli* Gaillard, p. 69, fig. 16; p. 70–72, fig. 17, pl. 3, figs. 24–25 and 26–27
1933 *Archaeotrogon zitteli* Gaillard, Lambrecht, p. 626
1971 *Archaeotrogon zitteli* Gaillard, Brodkorb, p. 246–247

MATERIAL: Early collections without provenance: almost complete left humeri, QU 15787, 15790, 15791, 15792a, 15792b, 15795; proximal left humerus, QU 15788; distal left humeri, QU 15784, 15793, 15947; almost complete right humeri, QU 15783, 15789, 15798, 15801; almost complete left coracoid, QU 15911; almost complete left carpometacarpi, QU 15647, 15927; almost complete right carpometacarpi, QU 15659, 15662, 15928, 15934, 15942, 15944; proximal right carpometacarpus, QU 15946 (Museum of Paris). Complete left humerus, PQ 1053, cast of no. 128 from the Museum of Munich, holotype; complete right humerus, PQ 1052, cast from the Museum of Munich (referred to *A. venustus* by Gaillard (1908), but its size actually corresponds to *A. zitteli*); distal right humerus, PQ 990; 3 left and 2 right tarsometatarsi, 4 of which are almost complete, PQ 1069 (One of these was figured by Gaillard (1908, fig. 16 and pl. 3, fig. 26–27) and attributed to *A. cayluxensis,* but it has suffered a little damage since then.) (Museum of Lyon).

Deposits of Pech du Fraysse: complete left carpometacarpi, PFR 11069, 11097; distal left ulna, PFR 11092 (Museum of Paris).

Deposits of Mas de Got B: complete left ulna, MGB 1548; complete right ulna, MGB 1555; almost complete left coracoid, MGB 1553 (University of Montpellier).

Deposits of Belgarite IVa: incomplete right humerus (University of Utrecht).

DESCRIPTION: According to Gaillard (1908:70), the humerus of *Archaeotrogon zitteli* is quite well distinguished anatomically from that of *A. venustus*. He stated that in *A. zitteli* the head of the humerus is much more widened transversely, the tricipital fossa is shallower, and on the anterior face, the bicipital surface is much reduced. I was able to study a large number of humeri of both species, and these morphological differences seem to me to be attributable to individual variation. The head of the humerus does not appear to be wider transversely, nor the bicipital surface smaller in *A. zitteli*. The tricipital fossa is perhaps slightly shallower in *A. zitteli,* but this character is rather variable. Certain specimens such as QU 15798 (Fig. 4d) have a shallow tricipital fossa, while others such as QU 15795 (Fig. 4c) have a much deeper tricipital fossa.

It appears to me that the principal character that distinguishes *A. zitteli* from *A. venustus* is size, the former species

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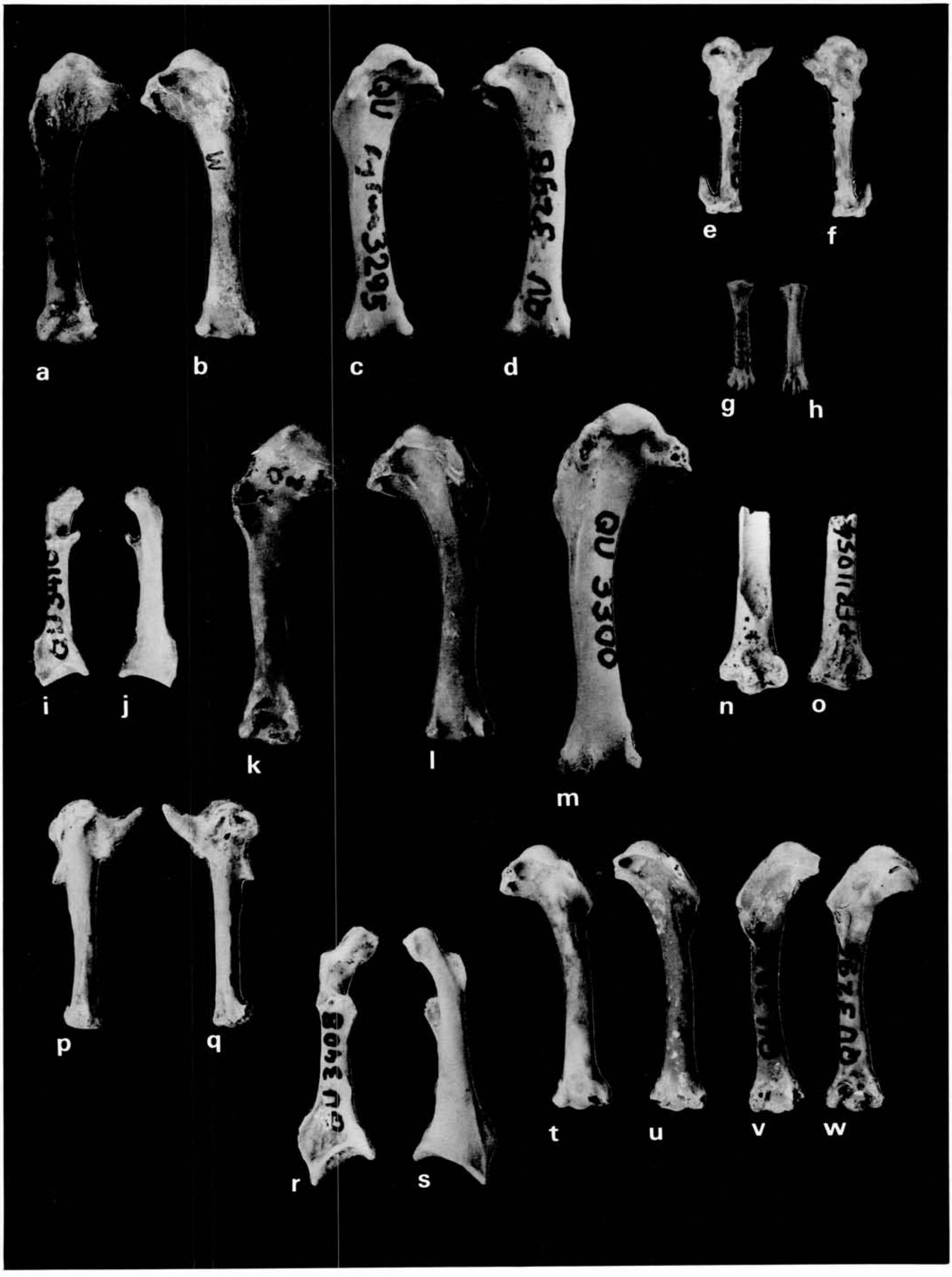
Figure 3. Specimens of *Archaeotrogon venustus*. Complete right humerus, QU 15782 (formerly QU 3282), Museum of Paris, ×3.9, in anconal (a) and palmar (b) view. Complete right coracoid, PFR 11168, Museum of Paris, ×3.6, in anterior (c) and posterior (d) view. Complete right ulna, PFR 11047, Museum of Paris, ×3.7, in external (e) and internal (f) view. Complete right carpometacarpus, MGB 1545, University of Montpellier, ×3.7, in internal (g) and external (h) view. Proximal right scapula, PFR 11254, Museum of Paris, ×3.6, in dorsal (i) view. Distal radius, PFR 11258, Museum of Paris, ×3.7, in external (j) and internal (k) view. Complete left femur, PFR 11082, Museum of Paris, ×3.7, in posterior (l) and anterior (m) view. Complete left tarsometatarsus, PFR 11091, Museum of Paris, ×3.7, in anterior (o) and posterior (p) view. Distal right tibiotarsus, PFR 11132, Museum of Paris, ×3.7, in anterior (q) view. Incomplete right tibiotarsus, PFR 11203, Museum of Paris, ×3.7, in posterior (r) view.

Table 2. Measurements (mm) of *A. venustus* and *A. zitteli* bones.

	Archaeotrogon venustus					*Archaeotrogon zitteli*				
	n	min.	max.	mean	variance s2	n	min.	max.	mean	variance s2
Humerus										
Length	20	25.0	29.7	27.82	1.31	12	30.1	33.4	31.43	0.84
Width head	27	8.4	9.4	8.85	0.07	9	9.4	10.3	9.98	0.06
Width distal end	56	5.8	7.2	6.30	0.11	16	6.8	7.5	7.13	0.03
Width shaft in the middle	92	2.6	3.3	2.91	0.02	18	3.2	3.7	3.48	0.03
Ulna										
Length	4	28.0	29.5	28.80	0.66	2	30.7	30.9	30.80	0.02
Width head	21	4.0	4.7	4.30	0.03	2	4.5	4.9	4.70	0.08
Width distal end	30	3.4	4.0	3.73	0.02	3	4.0	4.4	4.17	0.04
Depth distal end	30	3.6	4.2	3.84	0.03	3	4.1	4.3	4.20	0.01
Width shaft in the middle	39	2.0	2.4	2.17	0.01	3	2.3	2.4	2.33	0.003
Radius										
Width distal end	6	3.0	3.5	3.18	0.03					
Width shaft in the middle	6	1.1	1.2	1.17	0.003					
Carpometacarpus										
Length	21	17.8	19.8	18.84	0.18	10	19.5	20.9	20.27	0.36
Width head	32	6.2	7.8	7.08	0.20	10	7.5	8.3	7.85	0.08
Width distal end	25	3.6	4.5	4.01	0.07	7	4.0	4.8	4.46	0.08
Width metacarpal 2 in the middle	42	1.5	2.0	1.85	0.02	10	1.9	2.1	1.98	0.006
Coracoid										
Length	23	18.8	21.7	20.50	0.42	2	22.7	24.0	23.35	0.85
Width head	38	3.8	4.9	4.30	0.07	2	4.3	4.5	4.40	0.02
Width sternal end	19	4.7	6.2	5.34	0.16	2	6.2	6.2	6.20	0.00
Width shaft in the middle	46	1.9	2.7	2.22	0.03	3	2.3	2.6	2.43	0.02
Femur										
Length	5	22.0	22.4	22.34	0.16					
Width head	7	4.4	4.8	4.59	0.03					
Width distal end	7	4.2	4.5	4.36	0.01					
Width shaft in the middle	13	1.7	2.0	1.83	0.01					
Tibiotarsus										
Length	1			~29						
Width head	2	3.4	3.9	3.65	0.13					
Width distal end	4	3.7	4.1	3.83	0.04					
Width shaft in the middle	4	1.6	1.7	1.65	0.003					
Tarsometatarsus										
Length	2	16.2	16.6	16.40	0.08	5	15.8	16.7	16.26	0.15
Width head	3	4.0	4.4	4.23	0.04	4	4.0	4.2	4.08	0.01
Width distal end	5	3.8	4.1	3.96	0.02	4	3.8	4.5	4.18	0.09
Width shaft in the middle	7	1.7	1.9	1.79	0.005	5	1.9	2.3	2.04	0.02

→

Figure 4. Specimens of *Archaeotrogon. A. zitteli*: Complete right humerus, QU 15801 (formerly QU 3301), Museum of Paris, ×1.7, in palmar (a) and anconal (b) view. Complete left humerus, QU 15795 (formerly QU 3295), Museum of Paris, ×1.9, in anconal (c) view. Complete right humerus, QU 15798 (formerly QU 3298), Museum of Paris, ×1.9, in anconal (d) view. Almost complete left carpometacarpus, QU 15927 (formerly QU 3427), Museum of Paris, ×1.8, in internal (e) and external (f) view. Almost complete left tarsometatarsus, PQ 1069, Museum of Lyon, ×1.3, in anterior (g) and posterior (h) view. Complete left coracoid, QU 15910 (formerly QU 3410), Museum of Paris, ×1.7, in posterior (i) and anterior (j) view. *A. cayluxensis*: Complete right humerus, holotype, PQ 2, Museum of Lyon, ×1.7, in palmar (k) and anconal (l) view. Complete left humerus, QU 15800 (formerly QU 3300), Museum of Paris, ×1.9, in anconal (m) view. Distal right ulna, PFR 11054, Museum of Paris, ×1.9, in internal (n) and external (o) view. Complete right carpometacarpus, QU 15949 (formerly QU 3449), Museum of Paris, ×1.7, in external (p) and internal (q) view. Complete left coracoid, QU 15908 (formerly QU 3408), Museum of Paris, ×1.7, in posterior (r) and anterior (s) view. *A. hoffstetteri* new species: Almost complete right humerus, holotype, QU 15796 (formerly QU 3296), Museum of Paris, ×1.7, in anconal (t) and palmar (w) view. Almost complete right humerus, paratype, QU 15786 (formerly QU 3286), Museum of Paris, ×1.7, in anconal (u) and palmar (v) view.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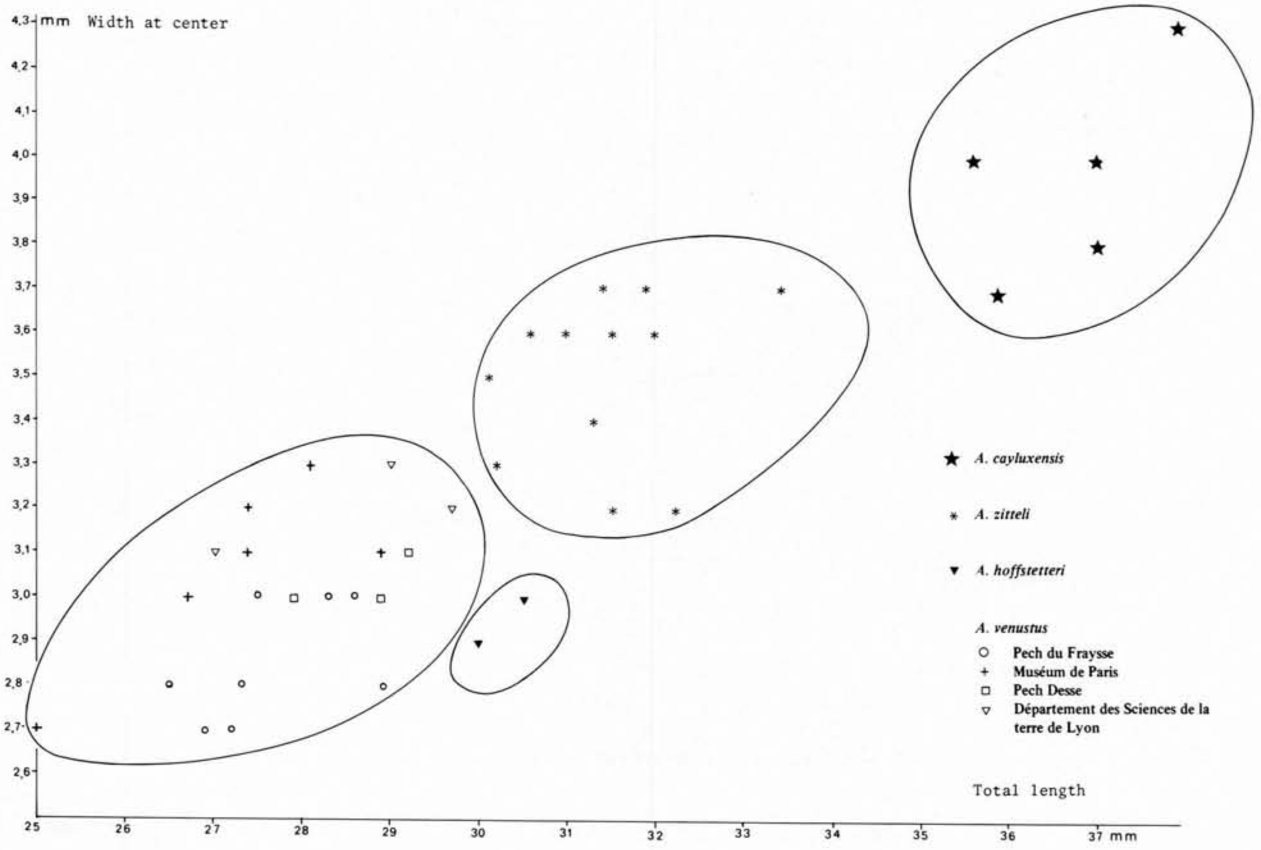

Figure 5. Scatter diagram for the humeri of the different species of *Archaeotrogon* from the Phosphorites du Quercy.

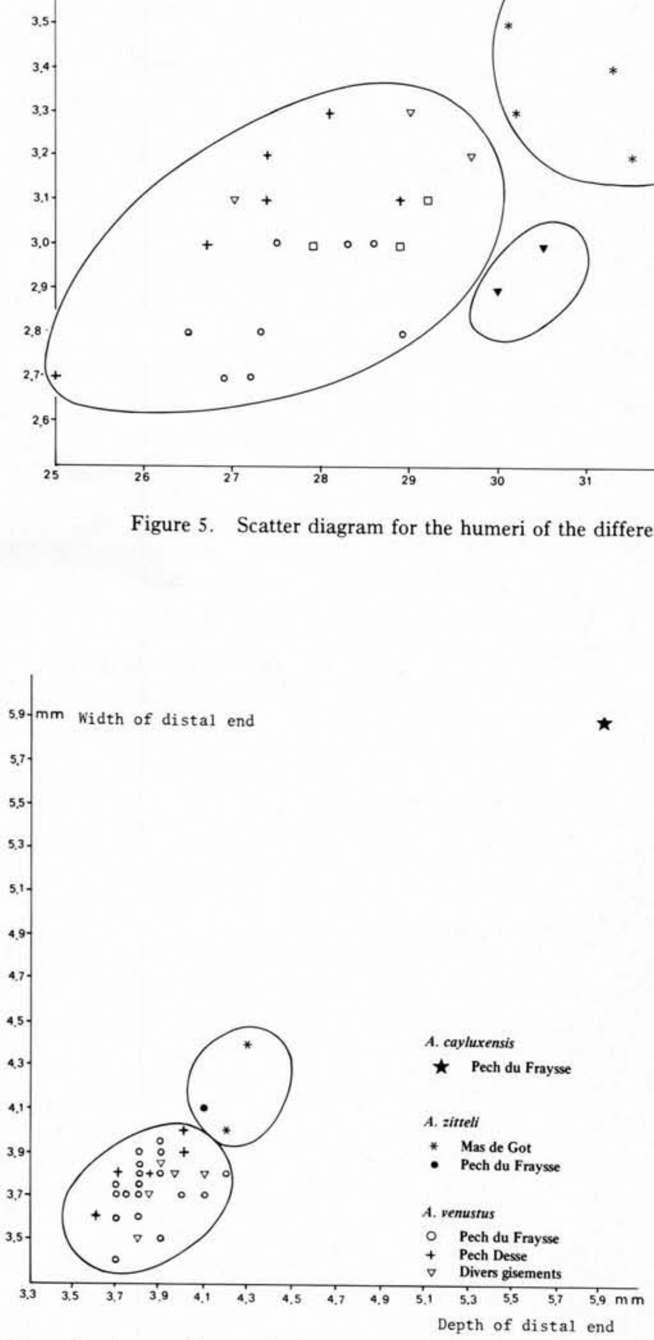

Figure 6. Scatter diagram for the distal end of the ulnae of *Archaeotrogon venustus, A. zitteli,* and *A. cayluxensis.*

being the larger. In the scatter diagrams (Figs. 5–9), they form distinct clusters of points. The measurements of the bones attributed to *A. zitteli* are shown in Table 2. They are slightly larger than those of *A. venustus,* and on the whole there is very little overlap in the measurements of the two species. This cannot be an example of evolution, i.e., the smaller *A. venustus* evolving into the larger *A. zitteli,* as both species have been discovered together in at least two sites in the new excavations at Quercy: Mas de Got B, of the lower Oligocene, and Pech du Fraysse, of the upper Oligocene.

I have referred to *A. zitteli* five tarsometatarsi from the Museum of Lyon (PQ 1069), one of which was figured by Gaillard (1908) and described as *A. cayluxensis.* The size of *A. cayluxensis* is much larger than that of either *A. venustus* or *A. zitteli.* Practically all the specimens of *Archaeotrogon* found at Pech du Fraysse belong to *A. venustus,* and it seems likely that the tarsometatarsi, especially the two complete ones (PFR 11091, 11175), likewise belong to this species. In the scatter diagram of the tarsometatarsus (Fig. 9), it is evident that the specimens numbered PQ 1069 have a total length comparable to that of the *A. venustus* from Pech du Fraysse, but their shafts are much thicker. It seems to me, therefore, that these tarsometatarsi belong to *A. zitteli,* all the more so since *A. zitteli* is far more numerous in the early collections than *A. venustus.* It is logical to assume that if one finds many humeri one should also have a few foot bones.

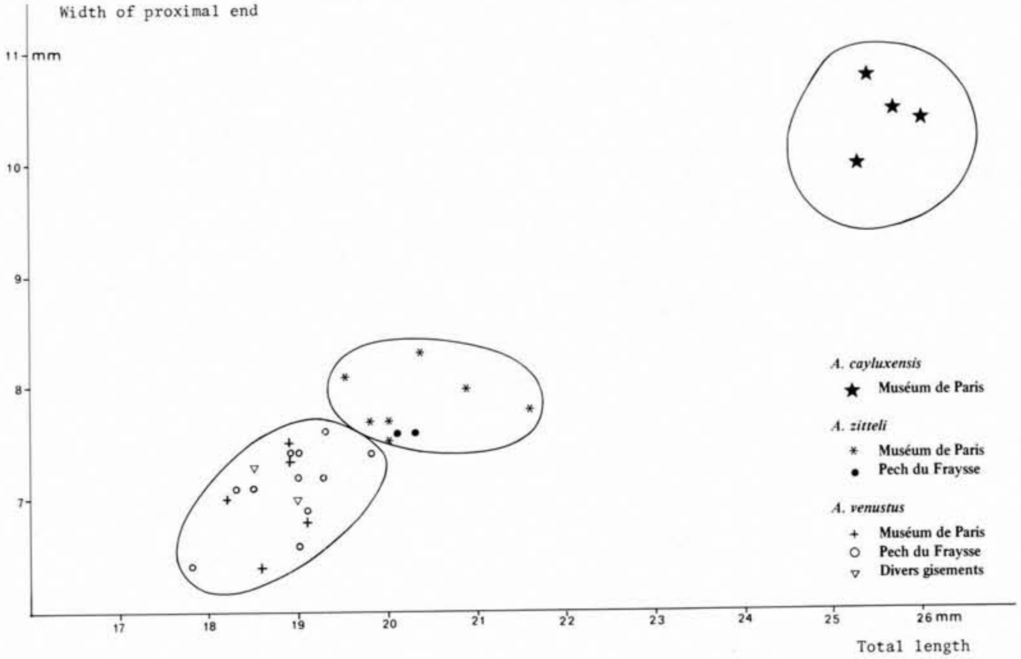

Figure 7. Scatter diagram for the carpometacarpi of *Archaeotrogon venustus, A. zitteli,* and *A. cayluxensis.*

Archaeotrogon cayluxensis Gaillard 1908

Figure 4k–s

1908 *Archaeotrogon cayluxensis* Gaillard, p. 67–70, fig. 15, pl. 4, figs. 1–4

1933 *Archaeotrogon cayluxensis* Gaillard, Lambrecht, p. 625–626

1939 *Archaeotrogon cayluxensis* Gaillard, Gaillard, p. 17–18, fig. 7

1971 *Archaeotrogon cayluxensis* Gaillard, Brodkorb, p. 246

MATERIAL: Early collections without provenance: almost complete left humeri, QU 15778, 15779, 15800; distal left humeri, QU 15780, 15803, 15806; distal right humerus, QU 15794; complete left coracoid, QU 15908; complete right coracoid, QU 15907; complete right carpometacarpi, QU 15916, 15924, 15948, 15949, 15950; proximal left carpometacarpi, QU 15668, 15944 (Museum of Paris). Complete right humerus, PQ 2 (Holotype of Gaillard); distal left humerus, cast without number (Museum of Lyon). Almost complete right humerus, figured in Gaillard (1939, fig. 7) (Department of Earth Sciences, Lyon).

Deposits of Pech du Fraysse: distal right ulna, PFR 11054 (Museum of Paris).

DESCRIPTION: Gaillard (1908:67) says that the humerus of *A. cayluxensis* differs from that of *A. venustus,* not only in size, but also in the following anatomical characters: in *A. cayluxensis,* the head of the humerus is thicker anteroposteriorly, the tricipital fossa and the sub-trochanteric fossa are large and shallow, the pectoral crest is long with a rounded edge, the bicipital surface is smaller in a vertical direction, the body of the humerus is more slender and widened toward the distal end, the epitrochlea and epicondyle are more prominent, and the inferior groove of the triceps is deeper.

Having been able to examine more material, certain of these distinctive characters seem valid and others less so. I would agree that the head of the humerus is thicker anteroposteriorly in *A. cayluxensis,* the bicipital surface is proportionately smaller, the epitrochlea and the epicondyle are more prominent, and the triceps groove is deeper. Further, the radial condyle is proportionately much more developed anteroposteriorly.

The form of the tricipital fossa is rather variable among individuals, being very shallow in the holotype, PQ 2 (Fig. 4l), but much deeper in other specimens, such as QU 15800 (Fig. 4m). The shape of the sub-trochanteric fossa appears no different than that of *A. venustus,* and the pectoral crest is not especially longer, nor is its border more rounded. The shaft is slender in the holotype, but it is much heavier in other individuals, for example, QU 15800 (Fig. 4m). It does not seem to widen more toward the base than does *A. venustus.* The most important distinguishing character is certainly the size, which is clearly superior to *A. venustus* and *A. zitteli* (Figs. 5–8).

Archaeotrogon cayluxensis is known mostly from the early collections. Only a single bone attributable to this species has been found in the recent collections from Quercy. It is a distal ulna from Pech du Fraysse (PFR 11054, Fig. 4n–o). Its morphology corresponds to that of the genus *Archaeotrogon,* and its size is very important (Fig. 6).

If one calculates the ratios of the means of the measurements of all the bones of the two species *A. cayluxensis* and *A. venustus,* the result varies from 1.28 to 1.52. If the same ratios are taken between *A. cayluxensis* and *A. zitteli,* the results vary from 1.14 to 1.43. This means that *A. cayluxensis* is an average of 1.28 to 1.52 times as large as *A. venustus,* and 1.14 to 1.43 times as large as *A. zitteli.* If one takes the only two measurements possible on the ulna from Pech du Fraysse and

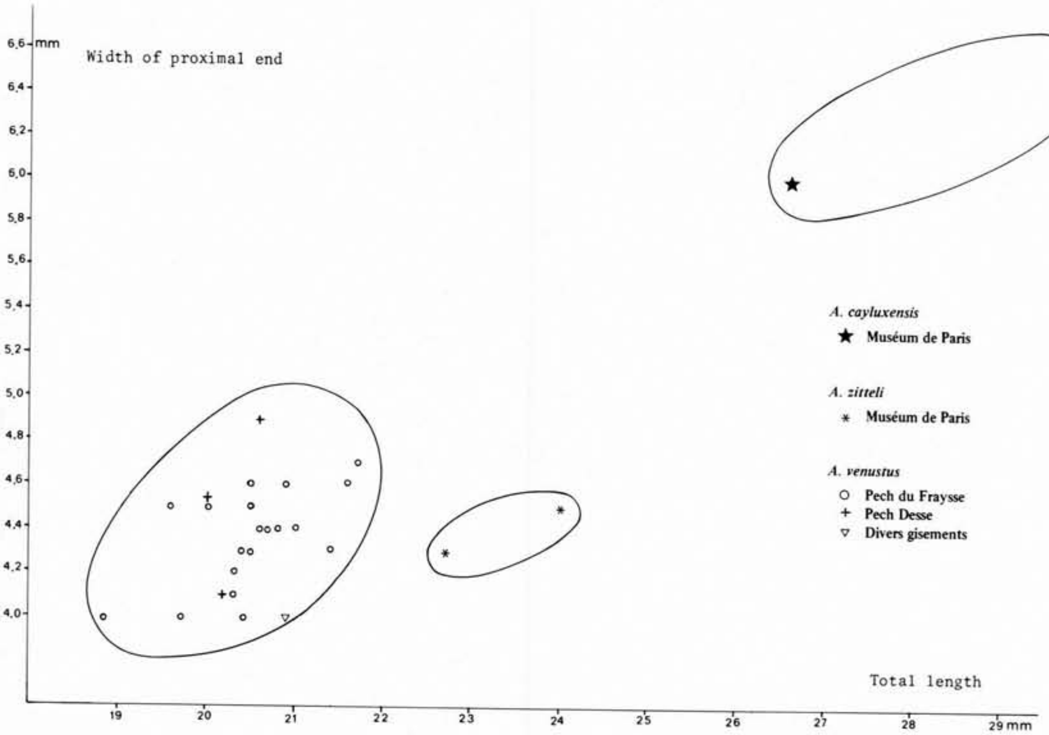

Figure 8. Scatter diagram for the coracoids of *Archaeotrogon venustus, A. zitteli,* and *A. cayluxensis.*

compares them with the mean values for the corresponding measurements of the other two species, the following ratios result: with *A. venustus,* 1.58 (depth) and 1.54 (width); with *A. zitteli,* 1.41 (depth) and 1.40 (width). The ratios between the measurements of the ulna from Pech du Fraysse and those of the other two species are therefore slightly larger than those generally observed between *A. cayluxensis* on the one hand, and *A. venustus* and *A. zitteli* on the other. But the ulna falls within the range of individual variation. It may belong to a particularly robust individual of *A. cayluxensis.*

MEASUREMENTS: For measurements of this species see Table 3.

Archaeotrogon hoffstetteri new species

Figure 4t–w

HOLOTYPE: Complete right humerus, QU 15796, National Museum of Paris.

PARATYPE: Slightly incomplete right humerus, QU 15786, National Museum of Paris.

TYPE LOCALITY: Phosphorites du Quercy, France.

TYPE STRATA: Upper Eocene or Oligocene.

DIAGNOSIS: A species of the genus *Archaeotrogon,* characterized by having a humerus of about the same size as that of *A. venustus* or *A. zitteli,* but with a much more slender

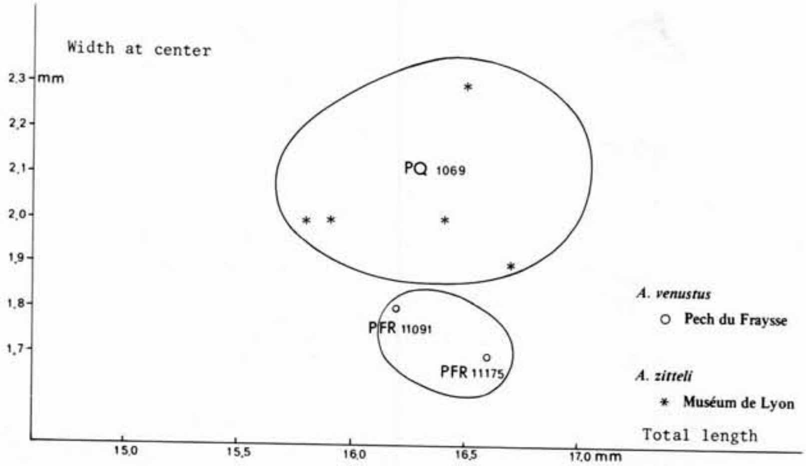

Figure 9. Scatter diagram for the tarsometatarsi of *Archaeotrogon venustus* and *A. zitteli.*

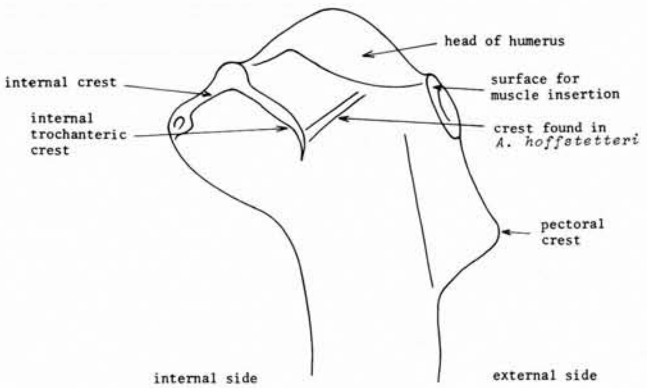

Figure 10. Diagram of the proximal end of the humerus of *Archaeotrogon hoffstetteri* new species, in anconal view.

shaft and with the proximal end much more recurved internally.

ETYMOLOGY: This species is named in honor of Dr. Robert Hoffstetter.

DESCRIPTION: These two humeri are sharply separated from the other humeri of *Archaeotrogon* by their slenderness and by the sigmoid curve of their shafts. Where the other humeri of *Archaeotrogon* are massive, these appear much more slender. Further, the proximal end of the bone is strongly twisted inwards.

On the posterior side of the bone, the tricipital fossa is very shallow. The sub-trochanteric fossa, under the internal trochanter, is bordered by two crests, an internal crest and a crest that Milne-Edwards called the internal trochanteric crest (Fig. 10). In *A. hoffstetteri,* another crest arises from the base of this internal trochanteric crest and leads toward the head of the humerus, crossing the tricipital fossa obliquely.

Below the external trochanter is a muscle insertion surface that is rather elongate and lies parallel to the long axis of the bone in *A. venustus, A. zitteli,* and *A. cayluxensis.* In *A. hoffstetteri* this surface is proportionately shorter and lies more obliquely.

In *A. hoffstetteri,* on the external face of the bone, the pectoral crest is very prominent and its upper edge shows a marked swelling. This pectoral crest is equally as prominent on the anterior side of the bone, and the bicipital surface is rather poorly developed.

The distal end of the bone does not show any particular characters, the more so since it is imperfectly preserved in both humeri attributed to this species.

RELATIONSHIPS AND DIFFERENCES: This species can be distinguished from *A. cayluxensis* by its much smaller size. The total length of the humerus is comparable to the largest among *A. venustus* or the smallest among *A. zitteli,* yet though the length is comparable, the shaft is far more slender in *A. hoffstetteri* (Fig. 5). Further, the bone has a characteristically sinuous shape. In addition, there are the other distinct morphological characters, i.e., a crest that obliquely crosses the tricipital fossa, the length and orientation of the muscle insertion scar below the external trochanter, and the very strong development of the pectoral crest in *A. hoffstetteri* (Fig. 10).

MATERIAL AND LOCALITIES: This species is represented only by the two humeri in the collections of the National Museum of Natural History in Paris, and is not represented in the newer collections from the Phosphorites du Quercy. The original locality is unknown, and it is impossible to assign it a precise geological age. It is possible that among the skeletal elements, other than the humeri, at present assigned to *A. venustus* and *A. zitteli,* certain bones may prove to belong to *A. hoffstetteri.* There is always the hope that this species may

Table 3. Measurements (mm) of *A. cayluxensis* and *A. hoffstetteri* bones.

	Archaeotrogon cayluxensis					*Archaeotrogon hoffstetteri*				
	n	min.	max.	mean	variance s2	n	min.	max.	mean	variance s2
Humerus										
Length	5	35.6	37.9	36.68	0.87	2	30.0	30.5	30.25	0.13
Width head	3	11.8	12.0	11.90	0.01	1			8.7	
Width distal end	10	7.5	8.5	8.18	0.12	2	6.3	6.8	6.55	0.13
Width shaft in the middle	10	3.7	4.3	4.05	0.04	2	2.9	3.0	2.95	0.005
Ulna										
Width distal end	1			5.9						
Depth distal end	1			5.9						
Carpometacarpus										
Length	5	24.7	25.7	25.42	0.24					
Width head	6	10.0	10.9	10.58	0.13					
Width distal end	4	4.9	5.4	5.13	0.05					
Width metacarpal II in the middle	6	2.4	2.6	2.53	0.01					
Coracoid										
Length	2	26.6	29.7	28.15	4.81					
Width head	2	6.0	6.6	6.30	0.18					
Width sternal end	2	7.4	8.8	8.10	0.98					
Width shaft in the middle	2	3.1	3.3	3.20	0.02					

Table 4. Temporal distribution of Trogoniformes in the deposits of the Phosphorites du Quercy. Mammal zones after Fahlbusch (1975).

	Stages and Absolute Age in my	Zones of Nannoplankton after Martini	Mammal Zones	Deposits of the Phosphorites du Quercy	Species of Trogoniformes
OLIGOCENE	Stampian	NP 24	Boningen	Pech du Fraysse	*A. venustus* *A. zitteli* *A. cayluxensis*
				Pech Desse	*A. venustus*
	26		Antoingt		
			Heimersheim		
		NP 23	Montalban	Itardies	*A. venustus*
				Mounayne	*A. venustus*
	32	NP 22	Villebramar	Mas de Got B	*A. venustus* *A. zitteli*
				La Plante 2	*A. venustus*
				Roqueprune 2	*A. venustus*
			Hoogbutsel		
	"grande coupure"				
EOCENE	36	NP 21	Frohnstetten		
	Priabonian	NP 20	Montmartre—San Cugat	Escamps	*A. venustus*
	39		La Débruge		
		NP 19	Perrière	Perrière	*A. venustus*
	41	NP 18	Fons 4		
	Bartonien s. st.	NP 17	Grisolles		

reappear in the course of new research on the phosphorites, and that we may then learn more of its skeleton.

MEASUREMENTS: For measurements of this species see Table 3.

TEMPORAL DISTRIBUTION

The distribution of the different species of the genus *Archaeotrogon* in the sites of the Quercy phosphorites is shown in Table 4. It is evident that *A. venustus,* which is the species most numerous in the recent collections, has a very large temporal range. It is already present in the Perrière zone, and persists at least until the Boningen, stretching across a length of at least ten mammal zones. In absolute terms this time span can be evaluated at nearly 15 million years.

The species *A. zitteli* and *A. cayluxensis,* quite common in the early collections, have been rediscovered in the course of the recent excavations in only two sites (Mas du Got B and Pech du Fraysse). It is therefore not possible to precisely determine their temporal distribution.

The Archaeotrogonidae are relatively rare, but are nonetheless found in beds antedating the "grande coupure," or "great change," such as those of Perrière and Escamps. This great change is practically on the Eocene-Oligocene boundary and is characterized by a large-scale replacement among the mammalian fauna. In the upper Eocene beds at Quercy, the predominant forms among the birds belong to the Aegialornithidae. In contrast, after the great change, it is the Archaeotrogonidae that become predominant while the genus *Aegialornis* disappears. The Aegialornithidae still existed, but they are represented only by the genus *Cypselavus,* which is always rather rare. As for the mammals, the "grande coupure" seems to correspond to a rather important change in the avian world.

ACKNOWLEDGMENTS

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A NEW MIDDLE EOCENE SHOREBIRD (AVES: CHARADRIIFORMES, CHARADRII) WITH COLUMBOID FEATURES

By Ella Hoch[1]

ABSTRACT: *Plumumida lutetialis* new genus and species is the third fossil bird to be described from the Messel site in West Germany. It is based upon a fractured postcranial skeleton and is referred to the Charadrii on the basis of numerous skeletal features. It deviates from all living and known fossil shorebirds by having a strong perching foot and skeletal structures in the pelvis and hindlimb considered to be connected with such specialization. By the form and supposed function of the foot the fossil bird shows similarity to the doves, but other dove apomorphies are lacking. Two skeletal features that may be autapomorphies for the group to which *Plumumida* belongs set the bird apart from the doves. *Plumumida* is believed to be related to those early shorebirds that are thought to have given rise to, among others, the doves; the genus is placed *incertae sedis* in the Charadrii. The depositional environment of the fossil is reviewed.

ZUSAMMENFASSUNG: Ein neuer Stelzvogel, *Plumumida lutetialis* gen. et sp. nov., wird als dritter fossiler Vogel aus dem Messeler Ölschiefer beschrieben. Die Art gründet sich auf ein postkraniales Skelett, das mässig verdrückt und unvollständing ist. Die osteologischen Merkmale deuten auf eine Verwandtschaft mit den Charadrii hin. Der Vogel unterscheidet sich jedoch von allen heutigen und fossilen Charadrii durch einen Sitzfuß. Zu einer solchen Spezialisierung passen auch die gefundenen Skelettstrukturen im Bein und Becken. In Form und mutmaßlicher Funktion des Fußes ähnelt *Plumumida* den Tauben, doch sind keine anderen Columbiformen Apomorphien am Fossil nachweisbar. Zwei Skelettmerkmale, die Autapomorphien der taxonomischen Gruppe sein könnten, zu der *Plumumida* eigentlich gehört, unterscheiden den fossilen Vogel von den Columbiformen. *Plumumida* ist zu den frühen (jungkretazisch-alttertiären) Stelzvögeln zu rechnen, aus welchen auch andere Formen, wie allem Anschein nach die Tauben, abgeleitet werden können. *Plumumida lutetialis* wird *incertae sedis* den Charadrii eingegliedert. Ein Überblick über die Lebens- und Einbettungsumstände des Fossils wird gegeben.

Two birds have previously been recorded from the Lutetian (Middle Eocene) deposits at Messel in the West German Bundesstaat Hessen. They are the alleged shorebird *Rhynchaeïtes messelensis* Wittich 1898, and *Diatryma* cf. *steini* Matthew and Granger 1917 (Berg 1965). The purpose of this paper is to describe a new shorebird from the Messel oilshale that is about the size of *Rhynchaeïtes messelensis,* but differs from that form in skeletal morphology and relative proportions, and from living shorebirds by having a perching foot.

The Messel site has yielded large quantities of fossil animal and plant remains, many of which have only recently been discovered. The total number of bird fossils so far secured from the site comes to over one hundred. Among these, more than fifty were kept by Frau E. Soergel in Freiburg im Breisgau (Tobien 1969:165), but these have now been returned to the Hessisches Landesmuseum in Darmstadt, West Germany, and about forty are under investigation by Dr. D.S. Peters at the Forschungsinstitut Senckenberg, Frankfurt am Main, West Germany. Such abundance, and the tragic fate now threatening the Messel pit from local authorities in one of industrial Europe's most densely populated areas, justifies a brief introductory description of the site.

THE MESSEL SITE

The Messel pit is located about 9 km NE of Darmstadt and 22 km S of Frankfurt am Main. It now appears as a 1000 by 700 m crater, 60 to 70 m deep, the bottom of which became covered by a shallow lake after mining was stopped in 1971 (Fig. 1). The pit was formerly exploited for oilshale, and produced about 1 million tons of crude oil used as fuel and for the manufacture of various products for the dyestuffs, electronics, chemical, and pharmaceutical industries until the site was closed down.

The oilshale was discovered in the mid-1870's, and exploitation began in 1886. The shale deposit is known to have had a maximum thickness of 190 m in the Messel pit, and there are other, smaller oilshale pits in the area. The shale occurred

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Figure 1. The Messel site at the end of February 1978. Photograph by J.L. Franzen (Senckenberg Museum, Nos. 296–297).

below Middle Eocene strata containing brown coal lenses up to 2 m thick (Franzen 1976a). Through the years 1886–1971, many specimens of fossil leaves, wood, insects, fish, frogs, tortoises, lizards, snakes, crocodiles, birds, and mammals were found and recovered by those working in the open air Messel pit (Tobien 1957), and by the Darmstadt Museum. Fossils were also obtained from the nearby Prinz von Hessen oilshale pit in the years 1912–24 (Franzen 1978). Unfortunately, because of the large water content (up to 40 percent) and the chemical constituents of the shale (marcasite in particular), combined with the state of knowledge of preservation techniques at that time, many of these fossils are now in a most miserable condition.

With the introduction of the "cast resin transfer method" (see Bornhardt 1975) developed in England in the 1950's (Toombs and Rixon 1950; see also Rixon 1976) and first applied to the Messel fossils by Dr. Walter Kühne in the early 1960's (Kühne 1961, 1962), a new period of preservation of the oilshale specimens began. The resin impregnates and locks the bones of one level of the fossils, thus hardening and supporting them sufficiently for further manipulation and studies, as well as for exhibition purposes. However, the parts of the fossil specimens that are not impregnated by the resin, or that do not adhere to it, are often lost.

A veritable fossil-rush followed the closing of the mine works in 1971. A multitude of collectors, most of them laymen, searched for traces of ancient life in the pit, not always to the good of the desired objects. Authorities finally had to take steps to safeguard, not so much the site, but the lives of the fossil hunters. At the end of 1974 the admittance of non-authorized persons to the site was prohibited.

Permission to collect fossils in the Messel pit was granted to the Hessisches Landesmuseum Darmstadt in 1913. This institution was the sole authorized collector until 1975 when the Forschungsinstitut Senckenberg, the University of Hamburg, and the Museum für Naturkunde Dortmund also obtained the right to conduct scientific investigations of the site. A large project is now in progress, financially supported by the foundation "Volkswagenwerk," involving many scientists and good amateurs working under the leadership of Dr. Jens Lorenz Franzen, Forschungsinstitut Senckenberg (Franzen 1978, 1979). More than 18,000 fossils have been recovered to date, the most conspicuous fossil group being perhaps the perissodactyls, *Propalaeotherium* spp. (first thoroughly described by Haupt 1925), although the holosteans *Amia* and *Atractosteus* (Lepisosteidae) and the salmoniform *Thaumaturus* are the most numerous vertebrates. Among the tetrapods, birds and bats dominate (Franzen 1979). A list of fossils is given by Koenigswald (1979). Several forms hint at a NW Europe–North American land connection that persisted until about the end of the Early Eocene (West et al. 1977; Berggren et al. 1978).

The fossils of the Messel oilshale are often, except for a certain flattening, exceedingly well preserved when found. Not only do major parts of bony skeletons occur, generally in articulation, but in many cases the specimens show substantial "shadows" of the organisms' soft tissues. Hair, feathers, and traces of colors in chitinous insect parts may occur at the site (Haupt 1925; Franzen 1976b, 1979). Even the cuticular structures of partly digested leaves in the intestines of some fossil herbivores can be studied in detail. For example, there have been investigations into the stomach contents of *Propalaeotherium messelense* (Franzen 1976b, Sturm 1978). These studies have, in turn, given material support to the hypothesis (first advanced by Kowalevsky 1873–1874; see also Strelnikov and Hecker 1968) of a habitat and food change during the evolution of horses (*sensu lato*) from pre-Miocene softground forests to grass plains, and from "omnivorous" to purely graminivorous equids, respectively.

Presented against this background, recent proposals for the future of the Messel pit evoke the quotation of a heading in the catalogue for the Senckenberg Museum Messel exhibition (Franzen 1977:24): "Wen interessiert eigentlich der Mageninhalt des Urpferdchens?"—"To whom is the stomach content of the protohorse of any real interest?" There are very few sites in the world where remains of an Eocene continental flora and fauna occur in such abundance and good state of preservation as at Messel. These fossils permit a multitude of scientific investigations and conclusions concerning evolution and the ecological, climatological, and physico-chemical aspects of the paleoenvironment. But, instead of preserving the Messel site and its fossils for the progress of knowledge, there are now official plans for the Frankfurt-Darmstadt-Dieburg-Offenbach metropolitan area to use the Messel pit for a large scale garbage disposal! This would also include so-called "non-dangerous industrial waste products." It may be true that large refuse accumulations are an inevitable result of modern environmental policy, but it is questionable if it is really necessary to install a giant garbage dump exactly in the Messel pit! Such shortsighted solutions to man-made problems are highly tragic, especially when viewed against the history of life.

AGE AND ORIGIN OF THE MESSEL OILSHALE

Judged from its fossil content, the bituminous deposit is of Lutetian age, 43 to 49 million years ago (Berggren 1972, and following the time scale agreed upon by workers presently studying the Eocene North Sea tetrapods in the "Projet 124 du Programme international des corrélations géologiques"). Tobien (1968, 1969:169) refers the oilshale to early Lutetian age on the basis of contained mammals. This is questioned by Franzen (1976a:422), however.

During middle to late Eocene times, Tertiary Europe experienced its maxima of temperature and marine transgression. Surrounded by the Atlantic Ocean, the North Sea, and the Tethys Sea, the two latter being connected over present-day Poland (Russell 1975; Bond 1978; Heissig 1979), the "Mid-European land" had a humid subtropical-tropical climate (Němejc 1970; Buchardt 1978), as is also indicated by the rich bitumen and lignite deposits formed at that time.

The Lutetian Messel lake and neighboring lakes developed concurrently with tectonic rifting of the area, as part of a larger river system (Tobien 1969). Detailed investigations, in particular of the location and orientation of fish fossils *in situ* in the oilshale, reveal the influx of two main water currents in the Messel lake, one from the northeast and another from the northwest, and the outflow of a current at the southern edge of the lake (Franzen 1979). Related studies (ibid.) have also shed light upon the distribution and probable local geographic derivation of the fossil organisms in the oilshale. The Messel flora and fauna were part of a warm, damp Eocene jungle environment. In its rivers and lakes the near-surface life was abundant, but the deep bottom waters were quiet and dark with anaerobic conditions. Thin strata of mineral particles and organic debris accumulated, embedding those parts of larger carcasses that were not devoured on their way down through the waters.

Towards the end of the Middle Eocene the lakes developed into swamps that were invaded by land plants. These plants gave rise to the lenses of brown coal that overlie the oilshale.

OTHER SITES IN WESTERN EUROPE WITH EOCENE BIRD REMAINS

European geography was subjected to great changes during Paleogene times. The interrelated Alpine folding and Rhinegraben rifting determined the formation of the central European tectonic features (Illies 1978; Illies and Greiner 1978), including the primary Messel lake. And North Atlantic rifting continued the rupture of the northern landbridge between Europe and North America. *Diatryma* occurred at Messel (Berg 1965), Geiseltal (Fischer 1967, 1978), and in France (Gaillard 1936) during the Middle Eocene, and is recorded from Upper Paleocene and Lower Eocene beds in north America and France (see Brodkorb 1967).

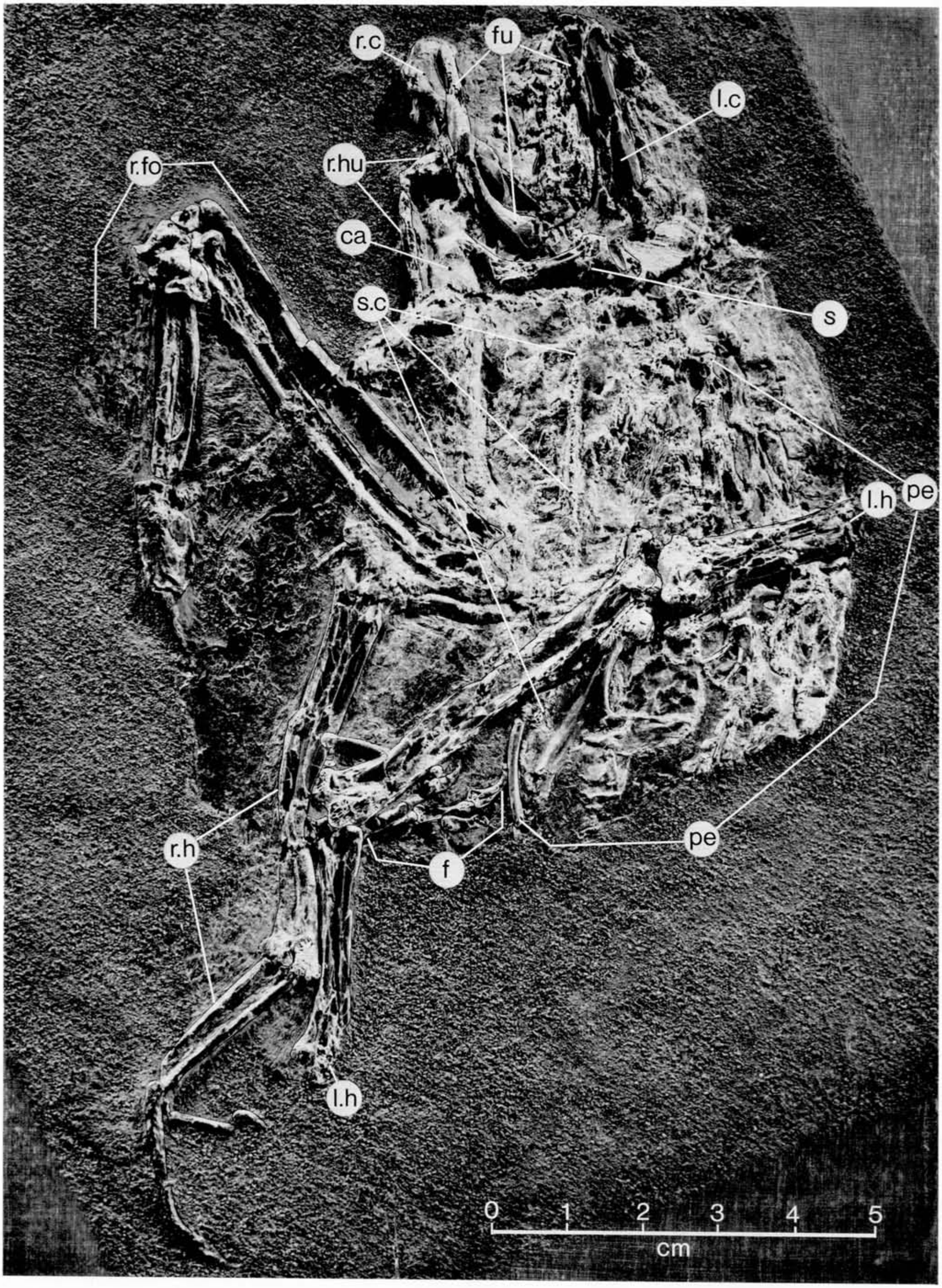
Briefly mentioned below are some Eocene sites in western Europe of interest to paleornithologists; faunistic or chronologic intercorrelations have not been made, nor have correlations with Eocene sites outside western Europe. Relevant literature older than that referred to can be found in the cited works.

British deposits yielding Eocene birds are known from the southeastern part of England; these fossils have most recently been discussed by Harrison (1971), and Harrison and Walker (1977). In France, Eocene bird remains are recorded from the Paris basin (Louis 1969; Brunet 1970; Hoch 1975); the bone-fissures of Quercy, or "les Phosphorites de Quercy" (Gaillard 1939; Collins 1976; Mourer-Chauviré this vol.); the Lower Eocene egg-bearing beds of Provence that are part of an upper Cretaceous–lower Tertiary series containing bones and eggshells of dinosaurs and eggshells of large birds (Touraine 1960, 1961; Dughi and Sirugue 1962); the Lutetian Strait of Carcasonne sediments with bird tracks (Plaziat 1964); and the sites that produced *Diatryma* referred to above. From Switzerland are known the Egerkingen siderolithic bone-fissures (Schaub 1940). A reputed bird-yielding locality in East Germany is Geiseltal, where fossils are occasionally even better preserved than in Messel (Lambrecht 1935; Fischer 1962). Fissure-fillings in the Schwäbischen and Fränkischen Alb in southern West Germany also contain bird bones (Dehm 1935). Within the Eocene North Sea area, fossil birds occur, outside England, at various sites in Denmark and northern Germany (Hoch 1975; the lower Mo-clay and Clay with Tuff deposits with bird fossils are now assigned to the Upper Paleocene, Hansen 1979).

GENERAL REMARKS ON THE FOSSIL BIRD AND ITS CLASSIFICATION

The specimen considered here (Fig. 2) is an incomplete, partially articulated skeleton of a small to medium size bird. It is flattened in an oblique, dorsoventral direction, and is shown from the ventral side in Figure 2. The dorsal side, the one exposed when the fossil was excavated, is now embedded in an artificial matrix (plast resin).

The right fore- and hindlimbs (Fig. 2, r.hu, r.fo, r.h) are turned out and rest beside the body. The left hindlimb (l.h) crosses over the abdominal area to lie alongside the right hindlimb. Soft tissue evidently still remained when the carcass was embedded in the lake sediments, and it determined the almost natural position of the limb bones relative to the body. The toe complex of the left foot (f) apparently became displaced not too long after deposition, and is now located around the distal end of the left tibiotarsus. No skull is preserved, which seems to be fairly usual for bird fossils from the Messel site (Franzen 1978:126). Other skeletal elements lacking or being unidentifiable in the fossil include most of the pre- and postsynsacral sections of the vertebral column, the ribs, the entire left forelimb, and two toes of the right foot. Generally speaking, the bones are fragmented and more or less incomplete, and their ends, in particular, are poorly preserved. In some places molds made of the embedding resin render the missing bone parts in indistinct contours. The state of preservation of the fossil seems similar to that described by Russell and Sigé (1970) for bats from the same locality.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In spite of its incompleteness, sufficient morphologic skeletal characters can be observed in the fossil for an allocation of the bird to taxonomic order. The concept presented by Bock (1974:383) at a symposium on contemporary systematic philosophies in 1973, advocating the presentation of the classification in the introduction instead of at the end of taxonomic papers, will be followed here: ". . . the reader [then] knows what statements are available for disproof, what tests will be attempted and hence why certain empirical evidence is being presented."

After comparison with relevant Recent and fossil birds, the specimen is referred to the Charadriiformes, and to the suborder Charadrii therein. Decisive for this taxonomic allocation is a suite of observable characters, which may or may not be unique for the Charadrii, but which taken together occur only within the group of birds traditionally regarded as shorebirds. I am here following Strauch (1978:270) when he states, referring to works by D.H. Colless, that one is forced to start with some sort of phenetic estimate of relationship as a beginning of a phylogenetic study. The fossil's state of preservation does not permit sophisticated morphologic deductions. Rather, it seems that the present paleontological work is one of those where, as pointed out by Cracraft (1972a:384), the use of overall resemblance is inevitable.

The fossil bird is considered to be related to those early Cenozoic "lapwings" and "coursors" that, according to Fjeldså (1976, pers. comm.), were specializing towards the sandgrouse/dove complex. In these "basal waders," the hindtoe had not been reduced and specialized to a cursorial life, as is the case in modern shorebirds. The Lutetian bird can be characterized as a robust member of the Charadrii with specializations simulating the doves: "a perching shorebird."

Features that refer the fossil to the Charadrii are:

1. A U-shaped furcula with a sturdy symphyseal part (Fig. 2, fu; Fig. 3, fu). In general morphology this latter part resembles those depicted by Strauch (1978: Fig. 22b, c) as typical of shorebirds. In doves, the furcula is weak.

2. A long sternal plate (Fig. 2, from s along the length of s.c), a good-sized carina with a distinctive pillar-like strengthening of the anterior edge (Fig. 2, ca, s.c; Fig. 3, ca, a.c), and the morphology of the anterior articular area. In ventral view the sternum shows, as exposed in the fossil, a fragmented strong anterior medial "lip" (Fig. 3, v.m), believed to be the base of a large ventral manubrial spine that overhangs the coracoidal sulcus (Fig. 3, c.s). The observable part of the sulcus for the left coracoid suggests a structure that was unbarred in lateroventral direction, and had a voluminous dorsal lip (see Description), both features also in harmony with shorebird morphology. No trace of a dorsal manubrial spine can be distinguished in the fossil, most probably because it was never there, which would agree with conditions in the Charadrii. In doves there are both ventral and dorsal manubrial spines, and the ventral one is small and does not "overhang" the coracoidal sulcus.

3. The relative proportions and the morphology of the wing bones (Fig. 2, r.hu, r.fo), in particular those of the hand. Part of the proximal end of the right humerus (Fig. 3, h.h, e.t, d.c) is preserved in the fossil. In the right elbow joint area (as determined by the position of the ulna and radius), there are crushed bone material and contours that are difficult to distinguish in the figures; these in all probability indicate the location of the distal end of the humerus. This will permit the statement that the ulna-radius segment is the longest of the forelimbs, with the humerus and hand segments about equally long and somewhat shorter than the ulna and radius (see Measurements below). Similar relative forelimb proportions are encountered in a large number of bird taxa, but other taxa differ from the common pattern, e.g., rails, where the humerus is longer, and doves, where the hand is longer. In doves the humerus is noticeably large and "swollen," but it is by far the shorter of the three mentioned segments. In the fossil, those traces of the humerus that are preserved testify to a fairly "ordinary" shape and to proportions corresponding to humeri in shorebirds (see Description). The carpometacarpus (Fig. 4, cm), by its long distal symphysis of metacarpals II and III, its fairly straight metacarpal III, and other morphologic features, suggests relationship with the Charadriiformes as well as with the Anseriformes. The strong basal part of metacarpal I (unfortunately its process is not preserved in the fossil), as pointed out to me by Jon Fjeldså, could very well indicate that this part of the carpometacarpus had a spur-like process as is found in, among others, many lapwings, and, as a potential preadaptation, throughout the plovers and allied groups. Such a character might not, however, exclude the Anseriformes from consideration, among which *Anseranas* has spurs on metacarpal I. The character may be primitive within the shorebirds, ducks, and a few other groups, corresponding to their supposed phyletic relationship and derivation from a common stock (Fjeldså pers. comm.). The observable morphology of the proximal phalanx of digit II (Fig. 4, d.II) corresponds to that in shorebirds such as *Vanellus* and *Pluvialis*. The element is believed to have been unfenestrated (a small hole (x) in the preserved lamellar bone in the fossil is a fracture), a state that excludes the bird from the Lari (Lydekker 1891), and in part the Glareolidae, within the Charadriiformes. There is general agreement that a non-fenestrated proximal phalanx of the hand-digit II (Strauch 1978:314: "digit III" error for digit II) is primitive in the Charadriiformes. The same element in doves shows a certain morphologic similarity to that in shorebirds but seems more "elaborated," with, e.g., the internus indicis process (corresponding to p, Fig. 4) much stronger than in unspecialized shorebirds, as is also indicated by Stegmann (1969:10 and Fig. 8). In doves the bone is also non-fenestrated.

The coracoids, pelvis, and long bones of the hindlimbs are reminiscent of those in shorebirds, but may at first sight be ascribed some dove traits. The coracoids (Fig. 2, l.c, r.c) are fairly long and straight with a short external lip of the glenoid facet (Fig. 3, g.l). Both in relative proportions and in detailed

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Figure 2. *Plumumida lutetialis* new genus and species. Holotype. Middle Eocene oilshale at Messel, Hessen, West Germany. S.G.P.I. Kat. Nr. 2183, Hamburger Geologisches Institut (Section of Palaeontology). The specimen is mounted on a slab of plast resin with a thin sediment coating. ca, sternal carina; f, toe complex left foot; fu, furcula; l.c, left coracoid; l.h, left hindlimb; pe, pelvis; r.c, right coracoid; r.fo, right forelimb, subelbow part; r.h, right hindlimb; r.hu, right humerus; s, sternum: anterior end; s.c, sternum: broken base of the sternal carina.

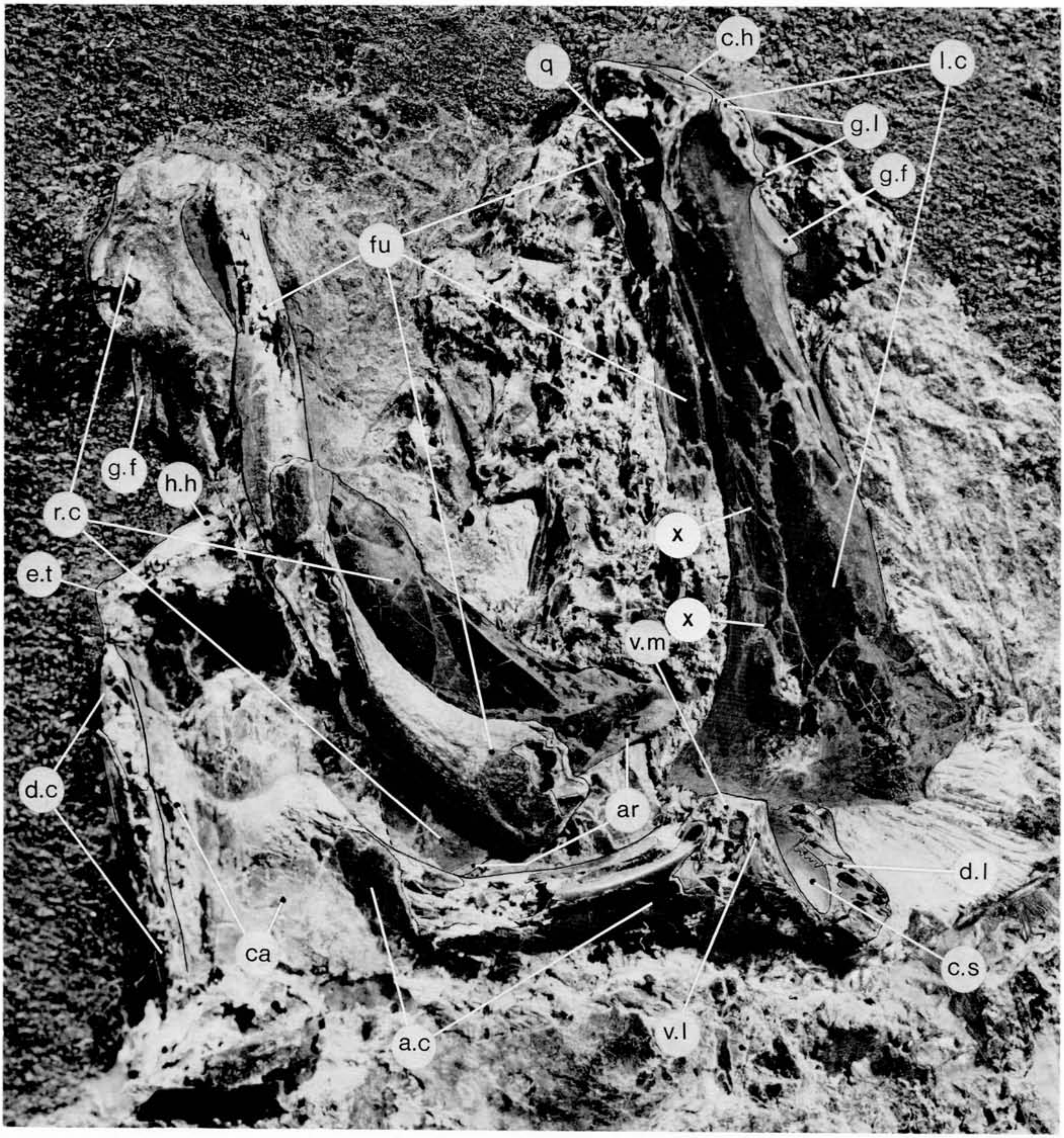

Figure 3. Shoulder girdle of the holotype of *Plumumida lutetialis*. a.c, anterior carinal margin of sternum; ar, articular markings at sternal edge of coracoid; ca, sternal carina; c.h, coracohumeral surface; c.s, coracoidal sulcus; d.c, deltoid crest of right humerus; d.l, dorsal lip of coracoidal sulcus; e.t, external tuberosity of right humerus; fu, furcula; g.f, glenoid facet; g.l, glenoid lip; h.h, humeral head; l.c, left coracoid; q, ?procoracoid; r.c, right coracoid; v.l, ventral lip of coracoidal sulcus; v.m, base of ventral manubrial spine; x-x, natural depression in coracoidal bone wall.

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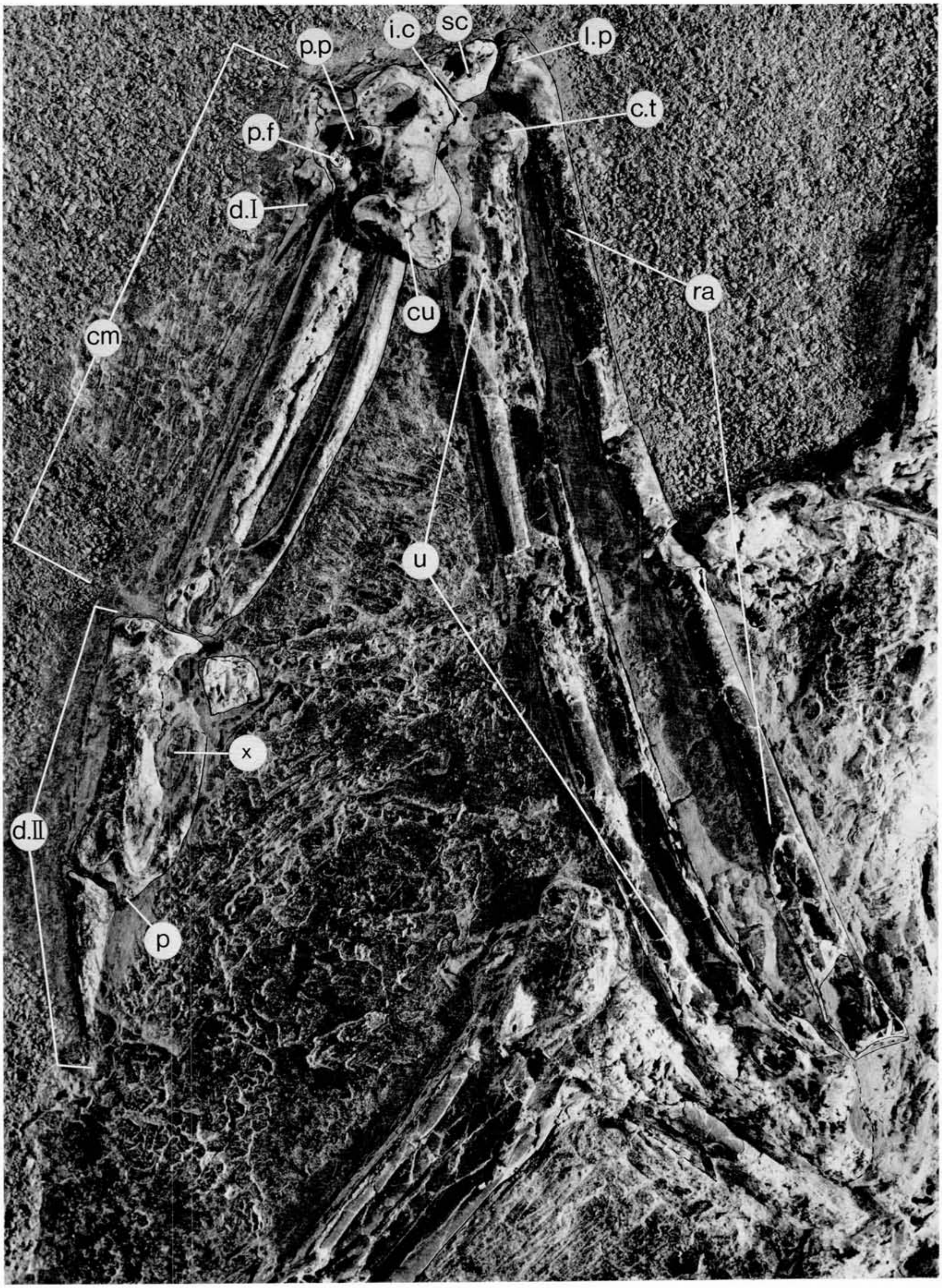
Figure 4. Right forelimb of the holotype of *Plumumida lutetialis*. cm, carpometacarpus; c.t, carpal tuberosity; cu, cuneiform; d.I, digit I; d.II, digit II; i.c, internal condyle; l.p, ligamental prominence; p, internus indicis process; p.f, process pertaining to pollical facet; p.p, pisiform process; ra, radius; sc, scapholunar; u, ulna; x, fracture in lamellar part of proximal phalanx of digit II.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morphology, as far as they can be discerned in the fossil, they are closer to those in shorebirds, e.g., *Charadrius,* than to those of doves (see Description). The pelvis (Fig. 2, pe) is a robust, short and wide element with distinct and fairly large iliac and ischiatic posterior processes. The robustness of the pelvis corresponds to that of the bones of the fossil in general. Robustness characterizes the pelvis, as well as the entire skeleton, of many doves, but such shorebirds as the oystercatchers, which some authors (e.g., Fjeldså pers. comm.) regard as primitive among Recent Charadrii, also have fairly robust skeletons. The visual impression of wideness of the fossil pelvis is exaggerated because of the flattened condition of the specimen. The shape of the posterior pelvic processes are, in fact, dove-like, as are some other details of the pelvis. The hindlimbs are dove-like, although some fine morphological features in the long hindlimb bones are shorebird-like. The relative proportions of the bones and the shape of the foot show similarity to the condition in doves.

The taxonomic status of the fossil at the family level has been subject to considerable circumstantial consideration. Judged from observed characters the bird does not fit into any of the generally acknowledged shorebird or dove families, and no living birds are found that exhibit intermediate shorebird-dove morphology (Stegmann 1969). Some paleontologists prefer the erection of a separate family for such a form, in order to (1) indicate that the bird is an aberrant but valid member of the order and suborder to which it is referred, and (2) secure it from being consigned to oblivion by being placed *incertae sedis* somewhere in the system when future reorganizers of the avian hierarchy find it a burdensome misfit. Another point of view is that such a monotypic bird family, based upon a single incomplete fossil exhibiting aberrant features, will be a nuisance to anyone who wants to make practical use of the bird system, and consequently that the bird should be included in one of the existing families.

According to Fjeldså (1976, pers. comm.) the early shorebirds, from which a coursor/sandgrouse/dove line can be derived, constituted the basic charadriiform group, together with the stone curlews that are close to the lapwings (compare Cracraft 1972b). Fjeldså groups some Recent Old World species (generally regarded as lapwings), which "must be very close to the basal late Cretaceous wader stock," in the genus *Xiphidiopterus,* while even the living stone curlews, oystercatchers, avocets, and certain others are "basal" in several aspects, although each group has its own specializations. Fjeldså's system is based on studies of Recent birds. It seems unjustifiable, on the basis of present evidence, to refer the Lutetian bird to any of Fjeldså's charadriiform taxa. The bird, by the structure of its foot, is evidently different from known shorebirds and their allies, the foot resembling that of doves. But a number of clearly apomorphic traits of doves (and sandgrouse and coursors) are missing. Reduction of the hindtoe is apparently habitually conditioned in plovers and other shorebirds: it tends to disappear in cursorial inhabitants of arid plains, whereas a small hindtoe remains in inhabitants of marshy environments (Fjeldså 1976). A well-developed hindtoe is considered a plesiomorphic character within the Charadriiformes, in accordance with Strauch's view (1978:320). The strong development of the hindtoe in the Lutetian bird, as part of a perching foot type, may be a plesiomorphic state. But rather, the whole foot structure should be regarded a specialization, paralleling that in doves, that sets the fossil bird apart from the Charadriidae *sensu* Fjeldså (including oystercatchers, stilts, and avocets). The fossil bird will be placed *incertae sedis* in the suborder Charadrii, a provisional status open to reconsideration when further evidence becomes available through new finds of fossil material. There are good possibilities for this, if paleontological work can be continued at the Messel site.

SYSTEMATICS

Order Charadriiformes

Suborder Charadrii—Shorebirds

Family *incertae sedis*

***Plumumida* new genus**

TYPE SPECIES: *Plumumida lutetialis* new species.

INCLUDED SPECIES: Type species only.

DIAGNOSIS: Shorebirds with a robust skeleton, the forelimbs longer than the hindlimbs. The coracoid has a long and distinct glenoid facet with a glenoid lip that is short in basal extension. The carpometacarpus has a distal metacarpal symphysis that is about one-fifth its length. The pelvis and hindlimbs show features reminiscent of doves. The synsacrum has the anterior part of the caudal section broad and flat ventrally, with two pairs of ventral parapophyses. The foot is a strong perching foot.

DISTRIBUTION: So far confined to the Middle Eocene (Lutetian) of Germany (BRD).

ETYMOLOGY: Latin, *pluma,* feather; and Latin, *(h)umida,* moist. The name alludes to the only true story we know of the bird, i.e., that it was post-mortem soaked in the Eocene Messel waters. The sound of the name may invoke the impression of the plumpness that characterizes the fossil bird skeleton, but it also conveys the feeling of the deep, dark mud that softly veiled the dead bird on the lake bottom and held it for over 40 million years.

***Plumumida lutetialis* new species**

HOLOTYPE: An incomplete, articulated, obliquely dorsoventrally flattened and partially crushed skeleton now preserved on a slab of artificial resin. Hamburger Geologischen Institut (Section of Paleontology), S.G.P.I. Kat. Nr. 2183; collected by Mr. Hans-Peter Schierning, Hamburg, West Germany, in 1972.

TYPE LOCALITY: The Messel oilshale pit, West Germany. According to the finder (letter of 24 November 1978): "Die Fundstelle liegt am westlichen Hang der Grube Messel auf der vierten Sohle des früheren Tagebaus. Die Schichten sind nicht bestimmbar, da eine Festlegung wegen fehlender Merkmale bisher nicht erfolgen konnte. Alle Ablagerungen fallen stark nach Osten ein."—"The fossil was found on the western slope of the Messel pit at the fourth exploitation level of the ancient open mine. The layers [with the fossil bird] cannot be correlated with others in the pit because stratigraphic indicators are lacking. All strata dip strongly towards the east."

DIAGNOSIS. As for genus.

ETYMOLOGY: Latin, *Lutetia,* Paris (that gave name to the Middle Eocene stage, the Lutetian, of western Europe);

and Latin, *-alis,* belonging to. In reference to the time when the bird lived.

MEASUREMENTS (in mm): Since all bones measured in the fossil are in some state of fragmentation and/or incompleteness, the measurements given are approximate. Shoulder girdle and forelimb: coracoid (shortest distance from top of bone to edge with sternal facet) 30; humerus (from top of head to elbow joint as determined by the proximal ends of ulna and radius) 58; ulna (maximum extension) 61; radius (maximum extension) 59; carpometacarpus (maximum extension) 34; phalanx 1 in digit II (length between metacarpal and digital facets) 15; total hand (from top of carpometacarpus to end of digit II) 58. Hindlimb: femur (see Description) 36; tibiotarsus (from proximal articular surface to, and including, distal condyles) 56; tarsometatarsus (maximum extension) 36; phalanx 1 in digit I 9.

DESCRIPTION: The bone terminology used is primarily that of Howard (1929).

The Shoulder Girdle. In this section of the holotype (Fig. 3), the furcula (fu) is seen displaced a little toward the right side of the bird relative to the coracoids, so that the right and median parts of the furcula are now resting on top of the right coracoid (r.c). The left furcular branch is located alongside the medial edge of the left coracoid (l.c). In the symphyseal region lies the anterior and stronger part of the sternum, turned out of its original position and partly crushed. The thickened anterior carinal margin (a.c) occupies a more or less transverse position in the figure, corresponding to an overturning of the carina toward the right side in the fossil. The left coracoidal sulcus (c.s) is exposed and can be followed into the matrix above the anterior part of the ventral lip (v.l). Mediad to the latter is the broken base of the ventral manubrial spine (v.m), as referred to above. The remains of the left dorsal lip (d.l) show that this structure attained its largest size toward the lateral termination of the coracoidal sulcus. The anteroventral termination of the carina is difficult to determine. Lamellar bone now adhering to the inner side of the deltoid crest (d.c) of the right humerus and covering the area between this and the anterior carinal margin is believed to belong to the carina (ca). Its natural edge is not preserved. Most of the carinal base (Fig. 2, s.c), including its triangular xiphial part (Fig. 2, lower s.c; Fig. 6, s.c), can be seen. Lamellar bone alongside the carinal base is either parts of the sternal plate or, as may be the case along its right side, remains of the overturned carina.

The coracoids are strong elements. Compared with coracoids in Recent shorebirds they seem little specialized in their sternal ends, where they show a similarity to the coracoids of such forms as *Haematopus, Pluvialis* and *Charadrius*. As seen in ventral view, their broader sternal part (not naturally delimited in the fossil in its present state of preservation) appears to have been moderately rounded from side to side, with a stronger rounding toward the medial edge of the bone. This is visible on the left coracoid, whereas the right one has suffered flattening in this area. The articular markings (Fig. 3, ar), visible in the right coracoid, are relatively small and almost identical in shape with those in *Haematopus ostralegus.* Toward the middle of the shaft, as seen in the left coracoid (Fig. 3, x-x), is a natural depression, also a morphologic correspondence with *Haematopus ostralegus.* An intermuscular line extends along the length of the bone (distinct in the left coracoid, Figs. 2 and 3). The humeral end of the left coracoid is comparatively well preserved, whereas in the right coracoid the humeral end is mainly in replica and shows no fine morphologic details of the original bone. In the left coracoid the glenoid lip (Fig. 3, g.l), of which only the base remains, is short in basal extension, and the neck of the bone, which is broken, diverges from the mainstem of the coracoid very close to its upper termination. The coracohumeral surface (c.h, only partially visible in the figure) is broad. The shortness of these structures is in contrast to the remarkably long glenoid facet (g.f) sharply set off from the surrounding bone wall. Bordering it sternally is a distinct, oblong-triangular sidewall of the coracoid. The structure indicated "q" in Figure 3 may be the distal part of the procoracoid.

The U-shaped furcula is very stout, or robust, judging from the preserved right side of its middle part and the remains of its branches. A ridge can be followed on the exposed surface of the bone, extending to the lower part of the symphyseal area. The ridge from right and left sides delimits a shallow symphyseal depression in the anterior wall of the furcula. No distinct furcular process can be observed.

The Forelimb. Part of the proximal end of the right humerus can be discerned (Fig. 2, r.hu; Fig. 3, h.h, e.t, d.c). And of the sub-elbow section (Fig. 2, r.fo; Fig. 4), the radius (Fig. 4, ra), ulna (u), cuneiform (cu), scapholunar (sc), carpometacarpus (cm), and digit I (d.I) and digit II (d.II) are comparatively well preserved. No trace is left of digit III.

The proximal end of the humerus is represented by the incomplete head (Fig. 3, h.h), external tuberosity (e.t), and deltoid crest (d.c). The external tuberosity is protruding, forming a "corner" or "shoulder" of the bone; in this character, the bone is similar to the humeri in shorebirds, but differs from those in doves. The base of the deltoid crest, as preserved in the fossil, appears broad and strong. It is fractured and apparently artificially widened, thus seeming broader than it originally was. It is about the same relative length as the deltoid crest in shorebirds. Possible crushed remains and vague imprints of the distal end of the humerus in the elbow area have been mentioned above. No bone fragments or structures in the area between the proximal and the presumed distal end of the humerus can be reliably referred to that bone.

The radius (Fig. 4, ra) and ulna (u) are fairly complete in outline, although their bone walls are fragmented and, especially in the radius, partially in replica. A fracture zone cuts across the middle of the radius and ulna, and disturbs the impression of the form of the bones. The radius was an almost straight bone with a swollen ligamental prominence (l.p). The ulna is crushed in its proximal end, where its limits can be traced against the background only with difficulty. In the distal end of the ulna, the carpal tuberosity (c.t) and internal condyle (i.c) are visible. The carpal tuberosity is a bulging structure with a large terminal ligamental attachment. The fossil ulna exhibits no papillar markings. The anconal papillae, if present, will be situated beneath the plast matrix.

The two free carpals, the cuneiform (cu) and the scapholunar (sc), are incompletely preserved. Compression of the specimen has caused a combined crushing and plastic deformation; where several bones were originally situated one on top of the other, their individual surfaces and limitations may now be difficult to trace in the fossil. This is evident in the wrist. The cuneiform *in situ* in the living bird is a U-shaped bone that

Figure 5. Pelvis of the holotype of *Plumumida lutetialis*. ?c.v, ?caudal vertebrae; d.p, dorsal parapophyses; f.h, head of right femur; fi, left fibula; l.f, left femur; l.il, left ilium; l.ti, left tibiotarsus; m, replica structure representing posterior synsacral vertebra(e); p. 1–3, lumbar parapophyses; r.il, right ilium; r.is, right ischium; r.pu, right pubis; 3.s, bases of third pair of single parapophyses in the caudal section of the synsacrum; s.c, xiphial part of sternum with broken base of sternal carina; s.p, sternal plate; sy.v, anterior synsacral vertebra; t.v, thoracic vertebra; v.p, ventral parapophyses; y, posterior iliac crest; z, interior pelvic ridge.

embraces part of the carpal trochlea, with one branch lying on the underside of the wing. This branch can be seen in the fossil, a little distal to its original position because of a 90 degree turning over of the bone. The other branch, beneath part of the carpal trochlea, supposedly together with the external condyle of the ulna, has been pressed into the trochlear bone material, causing a swelling proximal to the visible branch of the cuneiform. The deformed trochlear bone material is difficult to delimit from the fractured part of the cuneiform bone. Where unfragmented, the cuneiform shows a bulky shape with a median furrow, clearly visible in Figure 4, where may have lodged, judging from conditions in *Haematopus ostralegus,* the tendon that passes along the length of metacarpal II and fastens at the medial edge of digit II, together with (or forming part of) the exterior indicus longus tendon.

The carpometacarpus (cm), although easily identifiable in the fossil, is not too well preserved with respect to details. The trochlear section, as stated above, has suffered a good deal of deformation; the terminal parts of ridges and processes are lacking, as can be observed in the trochlear ridge, the process of metacarpal I, the pisiform process (p.p) and the process pertaining to the pollical facet (p.f). The shaft of metacarpal II is fractured, with part of the bone wall lacking or covered by plast matrix. The proximal part of the shaft of metacarpal III is in replica. And, in the distal end of the carpometacarpus, part of the bone wall is lost, and the tuberosity of metacarpal II is either lost or, as it appears, is covered by plast. The distal metacarpal symphysis is fairly long, surpassing in length that in some Recent shorebirds, including *Haematopus ostralegus* and *Charadrius hiaticula*. *Scolopax rusticola* has a similarly long distal metacarpal symphysis that might indicate that this condition is a specialized character within the shorebirds. In doves the distal metacarpal symphysis is short.

Digit I (d.I), the pollex, is recognizable in the fossil, but is incomplete. It has not been possible to free its distal end (if preserved) from the resin.

Both phalanges of the second digit (d.II) are relatively well preserved. The proximal phalanx, as mentioned earlier, is of some diagnostic importance within the Charadriiformes. The medial part of the bone is strong and forms the axis of the element, with strong and elaborate metacarpal and digital facets. The lateral part consists of a thinner lamellar section, laterally bordered by a thicker edge or rim. In the fossil, the proximal lateral part of the bone is lacking. Distally, the lateral bone section terminates in the internus indicis process (p) that in the living bird was connected by ligamental tissue to the distal end of the second phalanx, thus, together with the latter, forming a good support for the base of the distal remex. The chevron-formed mark close to the interphalangeal joint was the base for a strong tendon to the proximal edge of phalanx 2. This bone in the fossil is partly covered by resin and cannot be seen in its full extent. Remiges were also fastened to the upper side of phalanx 1 (and to the first finger, carpometacarpus, and ulna). Its elaborated and strong articular ends, well developed tendon mark, and entire morphology, reminiscent of that in shorebirds, together with the morphology of the other preserved bones of the wing and shoulder girdle, indicate that *Plumumida lutetialis* was a capable flyer.

A "stray" bone fragment occupies the original position of the third finger.

The Pelvic Girdle. A good deal of the pelvis (Fig. 5), including the synsacral (sy.v—m) and post-acetabular right portions (r.il, r.is, r.pu), is comparatively well preserved.

In the synsacrum, the sacral section is covered by part of the shaft of the left femur (l.f). A structure regarded to be the broken base of the posterior right parapophysis (p.1) of the lumbar section can be identified anterior to it (above it in the figure), together with the bases of the second-to-last (p.2) and third-to-last (p.3) right lumbar parapophyses. The bone wall of the right side of the corresponding part of the synsacral body is preserved, although fragmented, whereas most of the wall in the left side is in replica. The structure marked "sy.v" is considered to be the anterior synsacral vertebral element (or it may be the posterior free thoracic vertebra). In spite of fragmentation, its posterior limitation can be perceived; modern birds may also have a terminal marking of the first synsacral vertebra. Between this and the three lumbar synsacral elements, represented by their right parapophyses, are the remains of still another element. Thus intepreted, the number of presacral vertebrae included in the synsacrum is five. A fairly well preserved vertebral body (t.v) is closely attached to the anterior end of the structure marked "sy.v," but not fused with it as is seen from its position a little out of line with the synsacral axis, and from the presence of terminal bone walls in the intervertebral joint area. It has preserved a large right anterior projection for the support of the rib.

The pelvis in birds exhibits some individual variation in morphologic details (see also Boas 1933). Thus the number of synsacral thoracic vertebrae may vary within a species. One available pelvis of *Haematopus ostralegus* has five fused presacral vertebral elements, whereas another pelvis of the same species has four fused presacral elements and one vertebra whose body is not fused with the synsacrum, but whose transverse processes and ribs support the anterior parts of the ilia. The vertebral body structure marked "sy.v" in Figure 5 may not have been completely fused with the axial structures behind it, but its position suggests that it was part of the pelvis. Fragments of lamellar bone (s.p) situated along the right side of the axial structure in the fossil are most probably parts of the sternal plate and do not belong to the ilium, thus giving no indication of the anterior extension of the pelvis. The morphology of the presacral part of the synsacrum, as far as it can be observed, is reminiscent of that in shorebirds, although the elements are more robust in the fossil than in shorebirds. As stated for *Haematopus ostralegus,* the synsacrum in modern shorebirds may include five presacral vertebral elements. In some shorebirds, such as *Vanellus vanellus* and *Calidris alpina,* the number is generally four. The corresponding part of the synsacrum in doves is shorter and more compact than that in shorebirds, with only three, or in some cases four, included vertebrae.

Posterior to the superimposed left femur is the caudal section of the synsacrum (*sensu* Howard 1929). Anteriorly, in the fossil's right side, remains of two pairs of dorsal (d.p) and ventral (right v.p) parapophyses, and in the left side, the undisturbed proximal parts of two ventral parapophyses (left v.p), can be distinguished. The presence of both dorsal and ventral parapophyses shows that the corresponding two vertebral elements are the first and second synsacral caudal vertebrae. The number of ventral parapophyses in this region in birds is also subject to some intraspecific variation, so that, e.g., some members of a species that generally has only one pair of ventral parapophyses may have two pairs, or one pair and a right or left ventral parapophysis in front or behind it. The two pairs of ventral parapophyses in the fossil were strong structures, which indicates that they represent a normal condition of two pairs for this species. Fragmented remains of their distal ends in the right side show that the two ventral parapophyses of each side converged distally, where, as known from Recent birds, they joined the inside of the ilium, thus forming struts from the synsacral body to the acetabular region. The ventral wall of the anterior part of the caudal section of the synsacral body is broad and flat. It is only slightly disturbed in the fossil and thus gives a fairly correct idea of the morphology of that part in the living bird also. Posteriorly, remains of three pairs of "single" (i.e., not "split into" dorsal and ventral) parapophyses can be seen. No synsacral bone material was preserved posterior to the third pair of single parapophyses (3.s), and an indistinct replica contour (m) gives no morphologic details of the skeletal structure. But, judging from the shape of the neighboring part of the right ilium, which in the living bird was attached to the synsacrum, hardly more than one posterior vertebral element is lacking in the synsacrum. This would make six the number of caudal vertebrae included in the synsacrum. Fragmented bone walls remain in the two hindmost preserved interparapophyseal spaces (right side in the fossil), showing that these spaces in all probability were closed or nearly closed in the living bird. This also seems to have been the case in the most anteriorly preserved interparapophyseal space (between the double parapophyses). Matrix fills out the "background" in the intervening space, but lamellar bone fragments in the left side may also indicate the original presence of a bone wall in this interparapophyseal space. A structure in the fossil (?c.v), discernible in Figure 5 below and to the left of the caudal section of the synsacrum, is presumed to be the remains of the caudal vertebrae.

Most modern shorebirds have one pair of strong synsacral struts in the acetabular region of the pelvis, although two pairs of struts may occur. Doves have one, rarely two, pair(s) of comparatively weak synsacral struts. The number of synsacral vertebral elements posterior to the struts is generally four to five in shorebirds and five to six in doves. The interparapophyseal bone walls are usually fenestrated in the shorebirds, whereas in doves they tend to be closed.

The ilium, ischium, and pubis of each side are fused in *Plumumida lutetialis,* as are the corresponding bones in Recent birds. This leaves an ilio-ischiatic fenestra and a posterior incisure between the ilium and ischium, and an ischio-pubic fenestra or incisure between the ischium and pubis. Only fragments of the ilium (l.il) occur in the left side of the fossil. In the right side, because of compression, there is a large opening between the posterior part of the ilium and the synsacrum, which in many birds, including the shorebirds and (all?) doves, are not completely fused. The ilio-ischiatic fenestra has been closed by the ischium being pressed onto the lateral edge of the ilium (the presence of plast matrix obscures the details here). Most of the bone wall of the postacetabular part of the ilium is preserved (although fragmented), including a large posterior iliac process that in the present flattened condition exhibits transverse ripples, testifying to a certain degree of introflexion of the process in the living bird. The acetabulum has been protruded by the right femoral head (f.h), and the proximal parts of the right femur and of the left tibiotarsus (l.ti) and fibula (fi) have been pressed into the pelvic bone in the acetabular region causing fragmentation. The iliac bone wall between the distal ends of the right synsacral struts and the acetabulum is much disturbed and gives no information as to the original position of the struts relative to the acetabulum (see Strauch 1978:315). The interior pelvic ridge (z) has also been damaged in the acetabular region. The postacetabular part of this ridge, as far as it is preserved, is a strong and conspicuous structure in the fossil. It is almost straight, and continues posteriorly, where it is now broken, into the posterior ischial process. A bone structure beneath the posterior ridge fracture in the fossil may be the displaced fractured end of this process. Remains of a posterior iliac crest (y), which is the posterior limitation of the renal depression, can be observed connecting with the medial wall of the interior pelvic ridge. Along the lateral side of this latter structure is a fairly large lamellar bone wall of the ischium, somewhat disturbed by the xiphial part of the sternum (s.c). The preserved section of the right pubis (r.pu) indicates by its strength that the pubes were well developed, and apparently extended a good distance behind the medial part of the pelvis.

In many pelvic features *Plumumida lutetialis* shows good correspondence with conditions in doves. The innominate bone, as far as it can be studied, is close in morphology to that bone in, e.g., *Columba loricata.* The synsacrum, by its broad ventral wall of the anterior caudal section and apparently closed interparapophyseal walls, is reminiscent of the synsacrum in, e.g., *Columba palumbus.* The presence of two pairs of strong synsacral struts in the acetabular region is, however, atypical of doves. In some modern columbiforms the pair of main synsacral struts extends from the vertebral element anterior to that corresponding to the main strut element in shorebirds. Following Strauch (1978:314), the condition in these doves is the relatively derived of the two. He states (ibid.) that, in the most widely distributed and presumably primitive state for the Charadriiformes, the pair of main struts arises from the fifth vertebra from the posterior end of the synsacrum. The interpretation given above of the number of caudal synsacral elements in the fossil would permit the conclusion that the two pairs of synsacral struts in *Plumumida lutetialis* correspond to a combination of those of the shorebirds and those of the advanced doves. Thus, in this particular feature, *Plumumida lutetialis* may represent a form intermediate between shorebirds and advanced doves. Another interpretation is that both pairs of struts that may occur in specimens of modern shorebirds were strongly developed in *Plumumida lutetialis* as a consequence of the general robustness of the pelvis, which might also be said for other features that give the impression of strength. Recent shorebirds may have more than four, and doves more than five, caudal synsacral elements posterior to the strut element, suggesting that the number of caudal vertebrae included in the synsacrum is of limited diagnostic significance. Unfortunately, the sacral section, which would permit a correct determination of the homology of the vertebral elements in this region, is covered in the holotype.

The Hindlimbs. The greater portions of both hindlimbs (Figs. 5 and 6) are visible in the fossil, but their state of preservation permits few fine details to be studied. The right hindlimb (Fig. 6) is positioned in articulation with the pelvis, with the femoral head (f.h) located in the acetabulum as described above. Sections of the right femur (r.f) are seen as bone fragments or impressions in the matrix to the left of the superimposed left tibiotarsus (l.ti). The distal condylar part of the femur is crushed into more or less complete fusion with the crushed proximal articular part of the right tibiotarsus (r.ti). The femur length of 36 mm is measured between the visible extremes of the femur in the fossil, indicated in Figure 6 as the end points of the white lines "r.f." The original femur may have been slightly longer. In the proximal part of the right tibiotarsus, which is seen in anterior view, a distinct mark for the attachment of the M. flexor cruris medialis (f.a) can be observed. A ridge (on various fragments of bone), the intermuscular line (i.m), terminates proximally in the base of the (broken) inner cnemial crest (c.c). Because of the serious crushing of the proximal end of the tibiotarsus, the proximal continuation of the inner cnemial crest cannot be reliably indicated. A replica con-

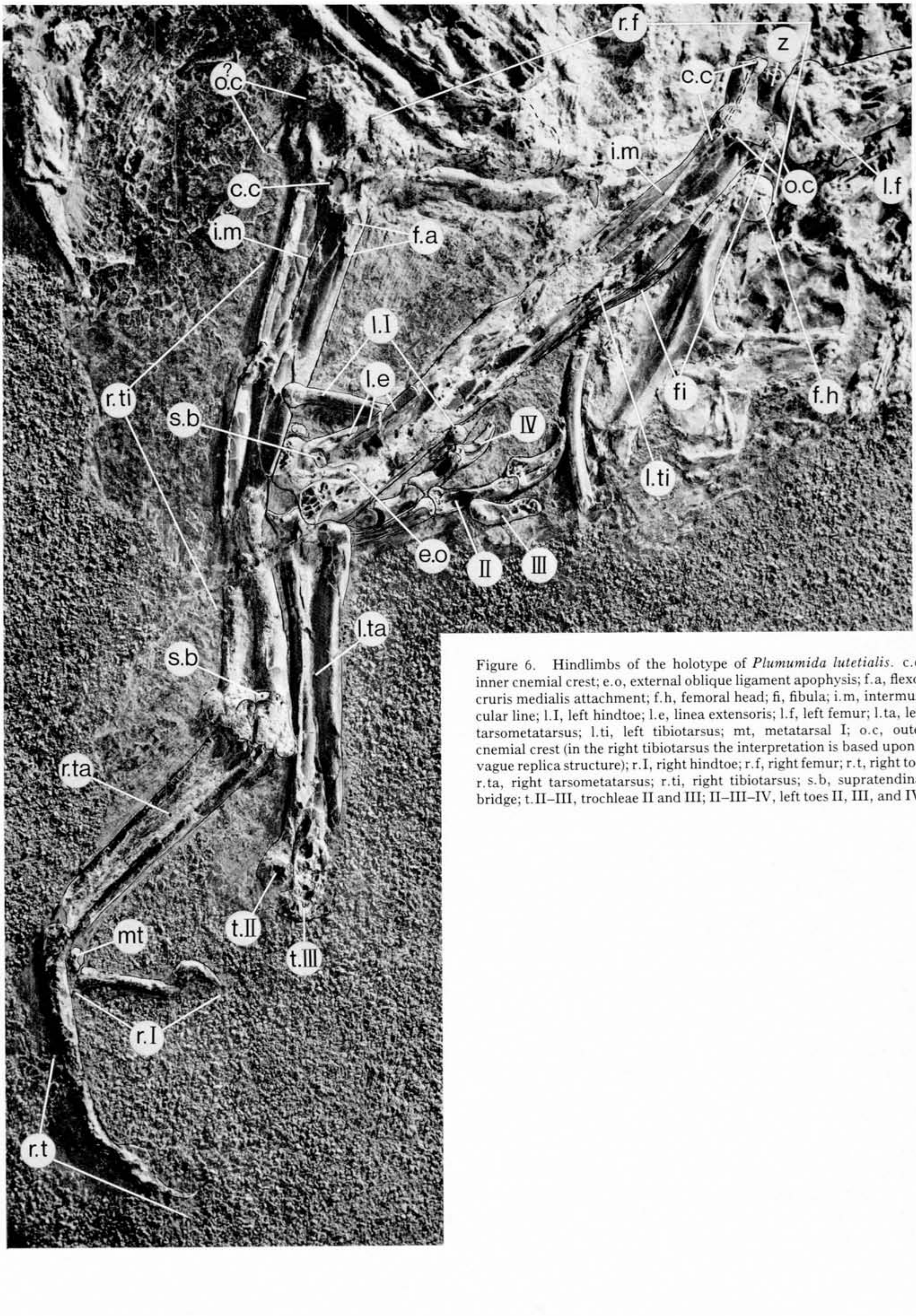

Figure 6. Hindlimbs of the holotype of *Plumumida lutetialis*. c.c, inner cnemial crest; e.o, external oblique ligament apophysis; f.a, flexor cruris medialis attachment; f.h, femoral head; fi, fibula; i.m, intermuscular line; l.I, left hindtoe; l.e, linea extensoris; l.f, left femur; l.ta, left tarsometatarsus; l.ti, left tibiotarsus; mt, metatarsal I; o.c, outer cnemial crest (in the right tibiotarsus the interpretation is based upon a vague replica structure); r.I, right hindtoe; r.f, right femur; r.t, right toe; r.ta, right tarsometatarsus; r.ti, right tibiotarsus; s.b, supratendinal bridge; t.II–III, trochleae II and III; II–III–IV, left toes II, III, and IV.

tour is tentatively interpreted as the imprint of the outer cnemial crest (?o.c). The shaft of the right tibiotarsus has undergone a special fragmentation because of lateral pressure from bones of the left hindlimb, resulting in a slight bending and some extension in a zone close to the present location of the proximal end of the left tarsometatarsus (l.ta), where little bone material is preserved. Part of the original bone wall remains near the distal end of the tibiotarsus, but around the intertarsal joint, most morphological details are obscured by intense crushing of the opposing ends of the tibiotarsus and the tarsometatarsus. One bone structure, the supratendinal bridge (s.b), appears strangely unaffected by the crushing. Rounded structures (set off in the figure) apparently represent the condyles. No trace of a right fibula can be seen. The remains of the right tarsometatarsus (r.ta) show an element with a wide median furrow. Some bone material is preserved, but most of the element appears in replica. Distally, the trochleae have not been preserved. Their termination was originally located a little distal to the base of the hallux (r.I). A fracture now occurs in the tarsometatarsus above the hallux articulation. The hallux, also in replica, has been determined on the basis of the presence of a small body (mt) interpreted as metatarsal I, and on the structure of the toe that seems to consist of one larger element and a curved and pointed distal segment, corresponding to the first and the ungual phalanges, respectively. The terminal structure (r.t), ending in a "claw," is also a toe replica, but the number of the toe cannot be determined since no reliable traces of articulation can be discerned.

In the left hindlimb (Figs. 5 and 6), the femur (l.f) is incompletely preserved, with the proximal part lacking, and the bone wall in the remaining part strongly fragmented. The left tibiotarsus (l.ti) is seen in its full length. Proximally, the base of the inner cnemial crest (c.c) can be traced, together with parts of the bone wall, medial and lateral to the crest. A broken structure (o.c) represents the outer cnemial crest. The bases of these two crests extend about similar lengths distad in the tibiotarsus. An intermuscular line (i.m) can be followed as a distal continuation of the inner cnemial crest for some length of the bone. The middle part of the shaft is much fragmented, with pieces of the bone wall lacking. Towards the distal end of the bone, a very clear linea extensoris (l.e) can be traced in three fragments, terminating distally in the broken internal oblique ligament apophysis. The external oblique ligament apophysis (e.o) is preserved in the fossil, as well as the supratendinal bridge (s.b). The distal condyles, although incomplete, are recognizable, as is the condylar fossa between them. Both condyles have suffered some deformation because of pressure against the surrounding bones. Sections of the fibula (fi) are preserved in what appears to be the complete original extension of the bone. Its proximal "head" is rather large.

The left tarsometatarsus (l.ta), in its exposed anterior side, has much bone material preserved. Proximally, the external cotyla has become somewhat deformed by the external condyle of the tibiotarsus being pressed into it. The internal cotyla is little disturbed. The depth and length of the anterior median furrow was artificially increased during the fragmentation of the bone by the left lateral wall being turned into the furrow. There was probably a median furrow in the upper part of the undisturbed tarsometatarsus, perhaps as wide as that seen in the remains of the right tarsometatarsus. But in the distal end of the bone, metatarsal III protrudes, thus making the front side of the bone convex. The remains of trochlea II (t.II) and trochlea III (t.III) show that the latter was the distalmost of the two, and presumably of all three trochleae. Trochlea IV is not preserved. No digits are found in natural articulation with the left tarsometatarsus, but partially articulated toe bones located around the distal end of the left tibiotarsus are considered to belong to the left foot. A long bone (left portion of l.I), situated transversely between the right and left tibiotarsi, is believed to be the proximal phalanx of the left hallux, corresponding in size to that in the right hallux (r.I). Its ungual phalanx may be the one exposing its hemispheric flexor tubercle (l.I), with a central foramen, close to the lateral side of the left tibiotarsus and pointing its distal tip along this bone in its proximal direction. Below it are two articulated toe structures that show strong, curved, and pointed ungual phalanges with transversely rounded undersides and deep lateral furrows. Four phalanges, of which the two middle ones are comparatively short, can be seen in one, and, in the other, two phalanges and the ungual phalanx are visible. In birds, four bones may occur in toes III and IV, and three bones may also occur in toe II. The interpretation of the two articulated toes shown in Figure 6 as toes II and IV, and the free phalanx representing toe III (or with numbers II and III interchanged) would correspond to conditions in, among others, doves.

No morphologic peculiarities of diagnostic interest can be studied in the fossil femora. The tibiae exhibit features that show similarity to the shorebirds and, for some of them, distinguish the fossil from the doves. In shorebirds, the M. flexor cruris medialis attachment is primarily a distinct oblong marking situated on the bone as it is in the fossil, whereas in doves the marking is different in shape, and is often more diffuse in outline than in shorebirds. Some shorebirds, such as *Vanellus vanellus* and *Calidris alpina,* have the bases of the inner and outer cnemial crests about equally long; this may, however, also be the case in some doves. The internal oblique ligament apophysis is in *Plumumida lutetialis* and Recent shorebirds situated rather closely above the level of the supratendinal bridge; in doves it is located farther proximad on the shaft of the bone. It appears in the fossil that the external condyle of the tibiotarsus is larger than the internal condyle; such is the case in shorebirds, but not in doves, where the internal condyle tends to be the larger.

The foot in *Plumumida lutetialis* is reminiscent of the foot in doves. Characters encountered in a moderately advanced perching foot include a relatively short and strong tarsometatarsus, and robust digits consisting of a long hallux and, as it also appears, three anterior toes of medium lengths, all with strong, curved, and pointed (although not to the extent seen in passeriforms or birds of prey) claws. Specialized perchers, as the Passeriformes, have all three trochleae of the tarsometatarsus in one line, whereas groundbirds, as the Charadrii, have trochlea III longer and more anteriorly protruding than trochleae II and IV (compare Stegmann 1969:25 ff). The dove foot seems intermediate in morphology and evolutionary stage between that in groundbirds of the shorebird type and the advanced perching foot.

The tarsometatarsus in Recent doves has no well developed anterior median furrow as has the tarsometatarsus in Recent shorebirds and, apparently, in *Plumumida lutetialis*. In doves the tarsometatarsus is shorter than the femur, whereas in shorebirds it is longer, in some cases much longer, than the femur. In *Plumumida lutetialis* the two bones are of about equal length. As stated above, Recent shorebirds exhibit various degrees of reduction of the hallux, showing that the plesiomorphic state in this group of birds is the presence of a hallux. In skeletal morphology and proportions the foot of *Plumumida lutetialis* appears to be intermediate between that of shorebirds and doves.

CONCLUSIONS

There seems to be fairly wide agreement that the Columbiformes developed from early Charadriiformes, perhaps during late Cretaceous times (for various elaborations of the idea, see cited works by Fjeldså and Stegmann, and works referred to therein). It is tempting, on the basis of the above description, to see in *Plumumida lutetialis* a form "on the line" from early shorebirds to doves. Only one pre-Lutetian columbiform, *Microena goodwini* Harrison and Walker 1977, described from the British Lower Eocene on the basis of a left tarsometatarsus lacking the trochlea for the 4th digit, has been recorded. Shorebirds are known as far back as the late Cretaceous (see Brodkorb 1967 and later works such as Brunet 1970 and Harrison and Walker 1976, 1977). *Rhynchaeïtes messelensis,* stated by Wittich (1898:144) to be intermediate between shorebirds and rails, is referred to the Scolopacidae by Brodkorb (1967) (on the basis of Wittich's investigations), an allocation that is, however, questioned by some workers.

Most features in the fossil specimen used to refer it to the shorebirds are believed to be plesiomorphic characters within the shorebird complex (i.e., the shorebirds and groups derived from them). A perching foot is a relatively apomorphic character therein.

Perching birds are found in various taxa of typically nonperching groups, such as the Cairinini within the Anseriformes, and *Anous* spp. within the Lari. In both the perching ducks and geese and the noddies, the hindtoe is markedly long and the claws are more robust than in other ducks and terns. The whole foot, however, is not very different from the foot in their close relatives. Yet it is said about the young of these birds that they have very strong claws and are good at climbing. Very advanced perching feet are encountered in the Passeriformes, less advanced in the Columbiformes. A perching foot with corresponding structural modifications in the hindlimb and pelvic girdle is a specialization that evidently developed more than once in bird history.

One feature in the fossil, the short glenoid lip-long glenoid facet structure in the coracoid, does not have a morphologic parallel in the investigated shorebirds and doves. Although encountered in other bird taxa, it seems to be unique for *Plumumida lutetialis* among known shorebirds and doves. The character is considered an autapomorphy for the taxon to which the fossil belongs.

The long distal metacarpal symphysis distinguishes *Plumumida* both from doves and from those shorebirds that are generally regarded as unspecialized. Specialized shorebirds, such as *Scolopax,* also have a long symphysis of the distal ends of metacarpals II and III. The character, presumably, is relatively apomorphic within the shorebirds, but is encountered within other bird taxa also.

Formally, following the above given statements, *Plumumida lutetialis* should be placed within the shorebird-complex as a separate taxon (because of autapomorphy) with sister-group status relative to either (1) the doves (synapomorphy: the perching foot), or (2) the *Scolopax* group (synapomorphy: the long distal metacarpal symphysis). For the present, however, acknowledging the incompleteness of the fossil, *Plumumida lutetialis* will be placed *incertae sedis* in the Charadrii.

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A NEW GENUS OF PENGUIN-LIKE PELECANIFORM BIRD FROM THE OLIGOCENE OF WASHINGTON (PELECANIFORMES: PLOTOPTERIDAE)

By Storrs L. Olson[1]

ABSTRACT: New specimens from the state of Washington, USA, and from Japan show that the family Plotopteridae Howard, previously known only from a portion of a coracoid from the early Miocene of California, consists of flightless Pelecaniformes, with the wing modified as a paddle remarkably convergent towards that of penguins and flightless members of the Alcidae. The Plotopteridae is rediagnosed and a new genus and species, *Tonsala hildegardae,* is described from a partial associated skeleton from the late Oligocene of Washington. Postcranial morphology shows the Plotopteridae to be closest to the Anhingidae, although the specialized spearing apparatus of anhingas is lacking. Plotopterids are known only from the North Pacific and only from deposits of late Oligocene to early Miocene age. The apparently simultaneous disappearance of the Plotopteridae in the Northern Hemisphere and the giant penguins in the Southern Hemisphere may be correlated with the rise of seals and porpoises. Brief comments are appended on convergence in the evolution of diving birds.

A little more than ten years ago, Hildegarde Howard (1969), in a brief and succinct note, introduced to science a new genus and species of bird, *Plotopterum joaquinensis,* based on the humeral end of a coracoid from an early Miocene deposit in Kern County, California. From this single specimen she concluded that *Plotopterum* should be made the type of a new family of Pelecaniformes, the Plotopteridae, related to anhingas and cormorants but with convergent similarities to penguins and alcids that suggested *Plotopterum* was a wing-propelled diver with a paddle-like forelimb. Although having no further information, Brodkorb (1971) assigned *Plotopterum* to a separate subfamily in the Phalacrocoracidae. However, subsequent discoveries of fossils from Japan and Washington have fully substantiated Dr. Howard's extraordinary perspicacity in recognizing the affinities and adaptations represented by the original fossil fragment.

Most of the new material of Plotopteridae, and also the best preserved, comes from several late Oligocene and early Miocene localities in Kyushu and Honshu, Japan, which I am studying in collaboration with Dr. Yoshikazu Hasegawa of the National Science Museum, Tokyo. We have summarized elsewhere some of our overall findings (Olson and Hasegawa 1979). The general nature of the Japanese specimens, with details of locality and stratigraphy, have been documented by Hasegawa et al. (1979). A more complete description of the Japanese material awaits preparation and study of recently discovered specimens. In the present paper I shall concentrate on the only specimen of Plotopteridae yet known from the eastern side of the Pacific, apart from the original fossil described by Howard.

The following diagnosis of the family Plotopteridae is based partially on characters ascertained from the as yet unnamed Japanese specimens, while that for the new genus is based on characters of the coracoid, the only element known for the sole taxon of the family hitherto named.

SYSTEMATICS

Order Pelecaniformes Sharpe 1891

In the following characters the Plotopteridae resemble the Pelecaniformes and differ from the Sphenisciformes and Charadriiformes: (1) absence of supraorbital furrows for salt glands; (2) deep transverse naso-frontal hinge; (3) sternum with large, pointed carina projecting far anterior to coracoidal sulci; (4) furcula articulating solidly by a large rounded facet with apex of carina (Fig. 1); (5) scapula with very large acromion projecting anteriorly well beyond coracoidal articulation; (6) coracoid with large flat furcular facet; (7) procoracoid process simple, without foramen (foramen lacking in certain alcids and incomplete in some penguins); (8) femur with proximal and distal ends proportionately broader, neck elongate; (9) internal condyle of tibiotarsus with marked medial deflection, and tendinal groove and openings wide; (10) tarsometatarsus with following combination of characters—metatarsals completely fused, hypotarsus with large medial crest, outer trochlea elevated well above others, inner trochlea elongate and at same level as middle trochlea.

Suborder Sulae Sharpe 1891

Family Plotopteridae Howard 1969

INCLUDED GENERA: *Plotopterum* Howard (1969); *Tonsala,* new genus; genus or genera unnamed (Japanese specimens).

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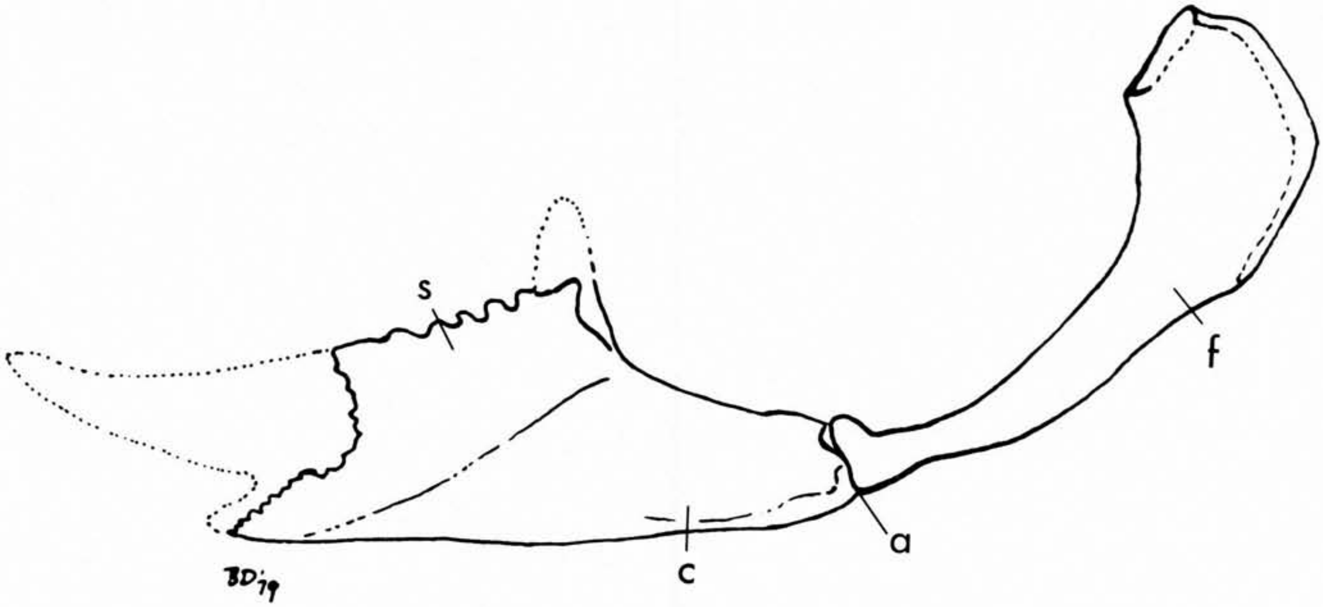

Figure 1. Right lateral view of the sternum (s) and furcula (f) in a plotopterid (specimen from Ainoshima Island, Japan), showing the far anterior projection of the carina (c) and its solid articulation (a) with the furcula, a characteristic of the Pelecaniformes.

DIAGNOSIS: Medium to extremely large, flightless, wing-propelled diving Pelecaniformes with forelimbs modified into penguin-like paddles. Humerus with shaft greatly flattened and curved, proximal end very heavy and rounded as in Spheniscidae, distal end appearing more similar to certain Alcidae. Ulna shortened, with row of distinct pits for attachment of secondaries. Radius flattened and expanded. Carpometacarpus short and flattened, with metacarpal I extending nearly half the length of the bone. Coracoid very straight and elongate; furcular facet projecting far ventrad; triosseal canal with lower part markedly convex, separated from glenoid facet by distinct longitudinal groove; procoracoid process long and acuminate. Scapula with blade thin and greatly expanded, somewhat as in Spheniscidae but acromion greatly elongated and narrow. Skull and cervical vertebrae not greatly narrowed and elongate as in Anhingidae; temporal fossae deep and postorbital processes large as in Sulidae. Caudal vertebrae very large. Pelvis broad and shallow with anterior portions of ilia expanded as in Anhingidae and Phalacrocoracidae; acetabulum lying entirely anterior to obturator foramen, unlike other Pelecaniformes. Femur and tibiotarsus most similar to Anhingidae. Tarsometatarsus somewhat similar to Anhingidae, but much heavier, not as excavated anteriorly, and with distal foramen continuous with intertrochlear notch.

TEMPORAL AND GEOGRAPHIC DISTRIBUTION: Known only from late Oligocene and early Miocene deposits of the North Pacific: Kyushu and Honshu in Japan; Washington and southern California, in the United States.

Tonsala new genus

TYPE SPECIES: *Tonsala hildegardae* new species.

DIAGNOSIS: Distinguished from *Plotopterum* by having coracoid with (1) glenoid facet more elongate, with margins not as distinctly raised above shaft, and (2) sternal margin not sinuate; (3) furcular facet projecting farther ventrad; (4) coracohumeral surface relatively longer and narrower.

ETYMOLOGY: Latin, *tonsa,* oar, and *ala,* wing, feminine; so named for the paddle-like development of the forelimb.

Tonsala hildegardae new species

Figures 2a–f, 3a–h, 4a–c, 5b

HOLOTYPE: Partial associated skeleton, vertebrate paleontological collections, USNM 256518. The specimen consists of the distal two-thirds of a right humerus, right ulna, proximal and distal ends of right radius, right ulnare and radiale, right carpometacarpus lacking most of the proximal end, proximal and distal (pathological) portions of left humerus and shaft of left ulna (pathological), humeral ends of right and left coracoids (both worn), right scapula, anterior portion of synsacrum, and right patella; also, several vertebrae, ribs, and unidentified bone fragments still in matrix. Collected 1 January 1977 by Douglas Emlong (field number E-77-1). The condition of the holotype suggests considerable predepositional breakage and wear of the bones, although some of the elements remained nearly in articulation. The left humerus is in two pieces, possibly due to a premortem break as the distal end is grossly pathological and so grown over with spongy bone as to be almost unrecognizable. Likewise, the left ulna appears to be atrophied. The specimen was preserved in an excessively refractory sandstone, necessitating laborious preparation by grinding.

DIAGNOSIS: As for the genus. Much larger than *Plotopterum joaquinensis*.

TYPE LOCALITY: Washington, Clallam County, Olympic Peninsula, south side of Strait of Juan de Fuca. On Disque Quadrangle, U.S. Geological Survey 7.5-minute series topographic map, 1950 edition, the locality is about 0.4 km E of first point of land extending into strait, slightly more than 3.2 km W of mouth of Lyre River, and immediately W of the mouth of Murdock Creek.

HORIZON: Late Oligocene, Pysht Formation of Twin River Group (see correlation chart in Snavely et al. 1978). Spec-

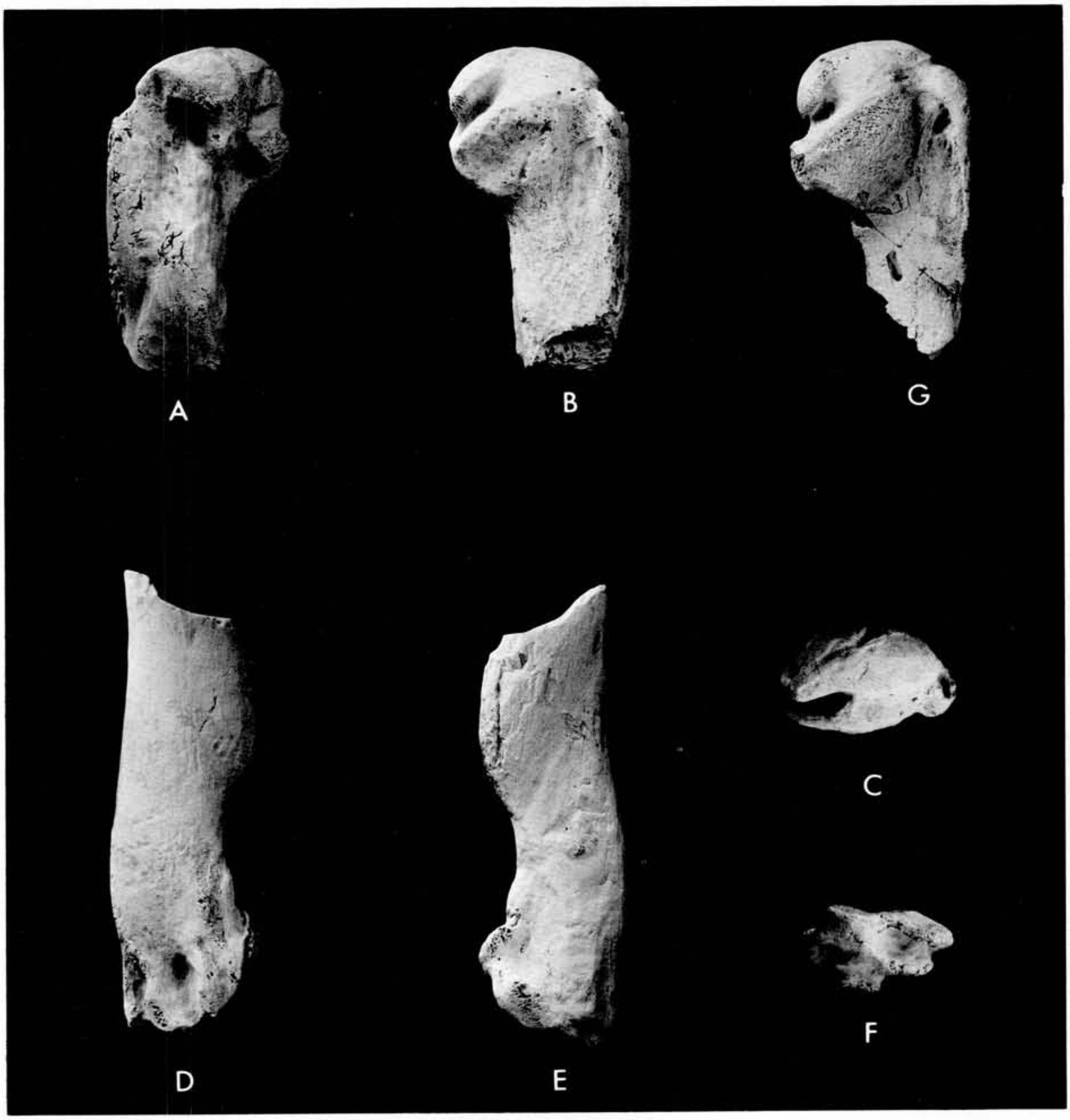

Figure 2. Humerus of *Tonsala hildegardae*, holotype (USNM 256518), and a late Eocene penguin. a, proximal end of left humerus of *Tonsala hildegardae*, external view; b, same, internal view; c, same, proximal view; d, distal portion of right humerus of *Tonsala hildegardae*, external view; e, same, internal view; f, same, distal view; g, internal view of proximal end of left humerus of a late Eocene penguin (gen. and sp. indet., USNM 244144) from Seymour Island, Antarctica, to show overall similarity in morphology to *Tonsala*. All figures ×1 except g, which is about ×½. The specimens are actually dark, but in this and the following two figures they have been coated with ammonium chloride to enhance detail.

imen found in float about 10 m from bank. Matrix barren of microfossils (C.A. Repenning pers. comm.). The locality is in the reference section of the "upper member" of the Twin River "Formation" in the terminology of Brown and Gower (1958). It is close to or at "locality A3690" of Durham (1944) and is in his *Echinophoria rex* zone. It is also very near or at "locality f 11810" of Rau (1964), regarded as upper Zemorrian in the California benthic foraminiferal stages. The most recent data would make the age of this deposit greater than 30 million years (Addicott 1977).

ETYMOLOGY: In honor of Dr. Hildegarde Howard, in recognition of her many contributions to the study of fossil birds, but more particularly of her correct diagnosis of an entirely new family from a single fragment of bone.

MEASUREMENTS OF HOLOTYPE (in mm): Humerus: proximal width 27.9, proximal depth 19.0, distal width (through external condyle) 22.7, distal depth (through internal condyle) 13.3, shaft width just distal to palmar crest 16.8, shaft depth at same point 7.9. Coracoid: distance from head to distal extent of glenoid facet 41.8, length of glenoid facet 24.6, breadth below head across triosseal canal 12.7. Scapula: total length (as preserved) 141.1, width at narrowest point 10.7. Ulna: length 72.5, proximal depth 18.7, proximal width 12.5. Carpometacarpus: distance from distal end of metacarpal

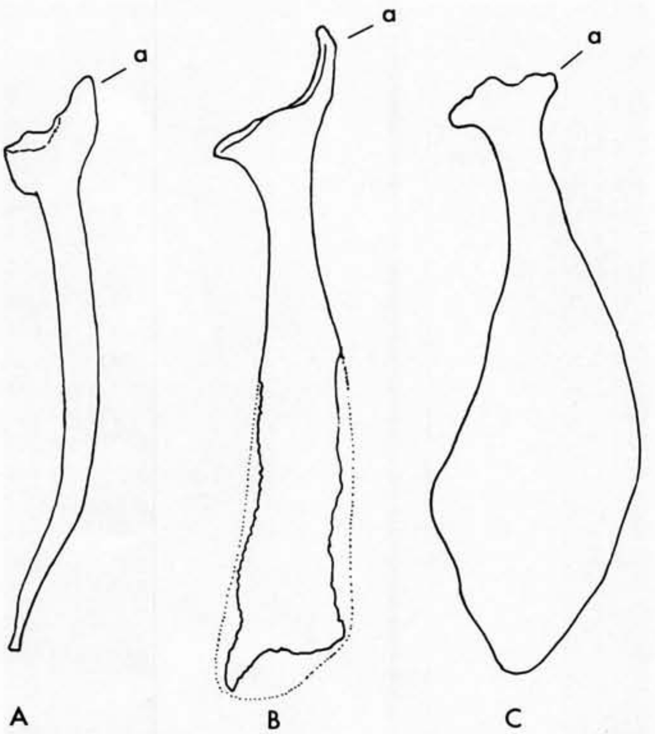

Figure 5. Ventral view of right scapula of (A) *Anhinga anhinga*, Anhingidae, Pelecaniformes; (B) *Tonsala hildegardae*, Plotopteridae, Pelecaniformes; (C) *Eudyptes chrysolophus*, Spheniscidae, Sphenisciformes. The acromion (a) is well developed in the two Pelecaniformes, in contrast to the penguin; however, the very broad but thin blade occurs only in penguins and the convergently similar Plotopteridae. Not to scale.

tion projecting anteriad as a distinct knob. In the Sulidae the patella is a more flattened, simpler structure, lacking the enclosed canal for M. ambiens. The patella in the Phalacrocoracidae, while varying within the family, is quite different, taking the form of a pyramid with a tetragonal base and projecting much farther anteriad than in *Tonsala*.

DISCUSSION

Tonsala hildegardae was a much larger bird than *Plotopterum joaquinensis* and also exceeded in size any of the living penguins except the two species of *Aptenodytes*. It is generically distinct not only from *Plotopterum,* but also from a much larger and as yet unnamed Japanese species for which comparable elements are known. The holotype of *Tonsala hildegardae* is the only specimen of bird yet known from the Oligocene marine deposits of the eastern Pacific. It is somewhat older than *Plotopterum joaquinensis,* but probably nearly contemporaneous with most of the plotopterids from Japan. In the deposits in which they occur, plotopterids are the only birds so far known. Yet they are absent from later deposits and thus evidently became extinct toward the end of the early Miocene. The giant penguins in the Southern Hemisphere died out at the same time. There is a strong possibility that the disappearance of these two unrelated groups in different hemispheres is linked with the contemporaneous ascendency of seals and porpoises (Simpson 1974; Olson and Hasegawa 1979).

The Plotopteridae not only belong in the Pelecaniformes, but are clearly derived from members of the suborder Sulae, which includes the Sulidae, Anhingidae, and Phalacrocoracidae. The species in the latter two families are entirely foot-propelled divers, but at least some of the Sulidae, all of which are plunge divers, are known to use the wings occasionally underwater to extend the depth of their dives (Thomas R. Howell pers. comm.). Increased specialization for such locomotion in some early pelecaniform group led ultimately to the development of the Plotopteridae.

In the course of modifying the forelimb into a paddle-like propulsive organ, plotopterids, penguins, and alcids have evolved numerous "shared derived character states," but only by blind adherence to cladistic methodology could these three families be classified as a monophyletic group. The profound differences between plotopterids and penguins or alcids and the many characters, including presumably derived ones, that link the Plotopteridae and the Pelecaniformes have been outlined above. To ignore such differences in favor of emphasizing similarities in what are clearly locomotor adaptations is to disregard the very information that leads to a true understanding of the evolutionary history of these taxa. This is nevertheless what Cracraft (1972:387) has done in attempting to resurrect the hypothesis that foot-propelled diving birds of the orders Gaviiformes, Podicipediformes, and Hesperornithiformes "evolved from a common ancestor" that was also a foot-propelled diver.

The physical constraints of extreme specialization of one or the other set of limbs for underwater propulsion obviously impose a certain morphological uniformity on those organs in the bird that happens to adopt such a mode of locomotion, regardless of relationships. Storer's (1960) analysis of evolution in diving birds, which does not ignore differences and which requires independent development of similarities in locomotor adaptations, is logical and in full accordance with observed facts. To this the Plotopteridae add a striking new example of the significance of convergence.

ACKNOWLEDGMENTS

Douglas Emlong collected, and G.B. Sullivan prepared, the holotype of *Tonsala hildegardae*. Emlong's field work was supported by a grant from the Smithsonian Research Foundation. Clayton E. Ray kindly provided detailed stratigraphic information. I gratefully acknowledge the cooperation of my colleague Yoshikazu Hasegawa, National Science Museum, Tokyo, who has supplied information, casts, and specimens of the Japanese plotopterids as well as much generous hospitality during my visit to Japan in 1976. Robert McKenzie, Natural History Museum of Los Angeles County, supplied a cast of *Plotopterum*. For their comments on the manuscript I thank John Farrand, Jr., Clayton E. Ray, and David W. Steadman. The line drawings are by Bonnie Dalzell. I am particularly indebted to Victor E. Krantz for his skillful photography of specimens.

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A NEW GENUS OF TERATORN FROM THE HUAYQUERIAN OF ARGENTINA (AVES: TERATORNITHIDAE)

By Kenneth E. Campbell, Jr.,[1] and Eduardo P. Tonni[2]

ABSTRACT: A review of the family Teratornithidae, heretofore known only from two genera and three species restricted to North America, is followed by the description of a new genus and species, *Argentavis magnificens,* from the Huayquerian (late Miocene) of Argentina. The new teratorn possessed cranial adaptations similar to those of *Teratornis merriami* L. Miller. It was approximately twice as large as *T. merriami,* with a probable wingspan of 6.5 to 7.5 m, the largest flying bird known to science. A possible second occurrence of a teratorn in late Pleistocene deposits of South America (La Carolina, Ecuador) is noted.

RESUMEN: Se realiza una revisión de la familia Teratornithidae, sólo conocida hasta el momento a través de dos géneros y tres especies restringidas a América del Norte. Se describe un nuevo género y especie, *Argentavis magnificens,* procedente de sedimentos de Edad Huayqueriense (Mioceno tardío) de la Argentina. Este nuevo teratorno poseía adaptaciones craneanas similares a aquéllas de *Teratornis merriami* L. Miller, siendo su tamano aproximadamente el doble que el de esta última especie. *Argentavis magnificens* tenía una envergadura probable de 6.5–7.5 m, por lo que representa el ave voladora de mayor tamaño conocida hasta ahora. Se hace referencia también a otro posible registro para un teratorno en el Pleistoceno tardío de América del Sur (La Carolina, Ecuador).

The teratorns are members of an extinct avian family, the Teratornithidae Miller 1925, long considered to be related to the New World vultures of the family Vulturidae. This relationship was based primarily on the raptorial appearance of the beak and certain parts of the postcranial skeleton, although it was questioned even as it was originally proposed (Miller 1909). All known species of the family were very large to gigantic birds, a fact that led many people to consider the teratorns as necessarily having a condor-like style of flying.

To date, the family Teratornithidae has been composed of only two genera, *Teratornis* and *Cathartornis*. The former contains two species, *Teratornis merriami* L. Miller 1909 and *T. incredibilis* Howard 1952. *Teratornis merriami* was the first described and is the best known species of the family, being represented by hundreds of specimens recovered from the asphalt deposits at Rancho La Brea, California, as well as specimens from other late Pleistocene localities in California, Florida, and Nuevo León, México (Brodkorb 1964).

In his original description of *Teratornis merriami,* Miller (1909:315) stated: "*Teratornis,* if it be considered raptorial, displays characters more or less distinctive of each of these groups [other families of the order Accipitriformes], though a preponderance of cathartid affinities is evident." While even then believing that *Teratornis* should be placed in its own family, he hesitated to take that step because of the lack of any hindlimb elements assignable to *T. merriami*. The following year, Miller (1910) described a new genus and species, *Pleistogyps rex,* based upon the hindlimb elements of *T. merriami,* an error he later recognized and corrected (Miller 1925:92). At that time, he established the family Teratornithidae, stating that "*Teratornis* . . . shows very bold divergence in its osteology from the closely knit family of the Cathartidae [=Vulturidae], the divergence taking a number of different pathways. The degree of divergence is in excess of those osteological differences to be noted between most families of living birds classified under one order" (Miller 1925:94).

Teratornis merriami was a very large bird, standing about 0.75 m tall, with a wingspan of 3.5 to 3.8 m. Early estimates (Fisher 1945; Stock 1956; Howard 1972) placed its weight at about 23 kg, but new data and calculations (John Anderson pers. comm.) indicate that 15 kg is a more accurate estimate. The California Condor, *Gymnogyps californianus* (Shaw), reaches a wingspan of 2.75 to 3.1 m and a weight of 9 to 10.5 kg (Koford 1953). Because of its size, it was long thought that *T. merriami* must have been a soaring bird, using wind currents and updrafts to maintain flight, much as the condors do. The tendency to equate large size with soaring flight probably played a significant role in maintaining the concept of *Teratornis* as a condor-like bird. After a study of the postcranial osteology, Fisher (1945) concluded that *T. merriami* was better adapted for flapping flight than condors. He suggested that the type of flight of *T. merriami* may have been similar to that in modern herons and pelicans, and also that it was not ca-

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pable of soaring under conditions that would keep *Gymnogyps* in the air indefinitely.

With this background, the discovery of the even larger *Teratornis incredibilis* was quite astounding. Unfortunately, *T. incredibilis* is known from only three specimens, none of which is particularly diagnostic. The species was named on the basis of a complete cuneiform bone from Smith Creek Cave, Nevada, a site that is "certainly no older than late Pleistocene" (Howard 1972:343). The second specimen referred to the species came from Irvingtonian deposits in the Vallecito Creek valley of the Anza-Borrego Desert, San Diego County, California. This specimen, a distal end of a radius, was referred to *T. incredibilis* "based on its general resemblance to that of *Teratornis merriami* and its tremendous size" (Howard 1963:16). The third specimen, the anterior portion of a beak, came from Blancan deposits in the Fish Creek beds of the Anza-Borrego Desert. This specimen was also referred to *T. incredibilis* on the basis of its general resemblance to *T. merriami* and its large size (Howard 1972).

Whether all of the three specimens referred to *T. incredibilis* are actually from the same species is problematical. As discussed by Howard (1972:343), if the three specimens are from the same species, its longevity would be in excess of three million years. However, these specimens are so undiagnostic that they may not even all belong to the same genus, much less the same species, and if they are all of the same species they may belong to a genus other than *Teratornis* (see Howard 1972:343). We hasten to add that we believe Howard's method of describing the specimens was most appropriate; she brought their existence to the attention of the scientific community, while at the same time leaving the resolution of higher level taxonomic categories until the discovery of more diagnostic material.

The three specimens referred to *T. incredibilis* are each approximately 40 percent larger than corresponding specimens of *T. merriami*. The large size of the cuneiform and radius indicates that *T. incredibilis* was a flying bird, and Howard (1952:52) has suggested that it had a wingspan of about 4.9 to 5.2 m, an estimate based upon the size of its cuneiform relative to that of *T. merriami*. *Teratornis incredibilis*, then, was rivaled only by *Osteodontornis orri* Howard 1957, a gigantic marine bird from the Miocene of California, for the title of the world's largest flying bird. Howard (1957:15) suggested that *O. orri* may have had a wingspan near 5 m.

The genus *Cathartornis* is composed of only one species, *C. gracilis* Miller 1910, a taxon based upon two tarsometatarsi from Rancho La Brea, California. In a reevaluation of *C. gracilis*, Miller and Howard (1938) considered it to be generically distinct from *Teratornis*. They also considered *Teratornis* and *Cathartornis* to be sufficiently similar to warrant the transfer of the latter from the Vulturidae, wherein it was originally placed, to the Teratornithidae. Based upon the size of the tarsometatarsus, which is as long as but more slender than that of *Gymnogyps californianus*, *C. gracilis* is the smallest of the known teratorns.

Brodkorb (1964) reduced the Teratornithidae to subfamilial rank within the Vulturidae. On the other hand, Jollie (1977:111) considered *T. merriami* to be "the most extreme cathartid in some respects" and the teratorns to be distinct at the familial level within the Accipitriformes. Olson (1978:168), however, has suggested that the teratorns may be a pelecaniform group. This suggestion was based in part upon the shape of the sternum of *T. merriami*, about which Fisher (1945:727) noted, "There is nothing cathartid about this bony element . . . " The senior author of the present paper recently initiated detailed studies of the osteology of *T. merriami*, with the intended goal of further determining its functional morphology and phylogenetic relationships. Preliminary results indicate that *T. merriami* was condor-like in its locomotory but not its feeding behavior, and that the teratorns may not be related to any of the families of Accipitriformes. In fact, *T. merriami* does have many structural similarities to pelecaniform birds, both in its cranial (as noted below) and postcranial osteology. However, these similarities appear to be a result of convergence and probably do not reflect phylogenetic relationships.

In summary, the Teratornithidae has been comprised of three species of very large to gigantic flying birds placed in two genera, all known from North America. Two of the species, *Teratornis incredibilis* and *Cathartornis gracilis*, are known from only a few specimens, and may or may not be related to *T. merriami*. The latter is known from hundreds of specimens, but its physical characteristics and relationships with other avian groups are still poorly understood.

To the Teratornithidae we can now add a new genus and species of such staggering proportions that one can only marvel that such a bird could have existed, and at the good fortune of finding a fragmented associated skeleton of it.

SYSTEMATICS

Order Accipitriformes (Vieillot 1816)
Family Teratornithidae L. Miller 1925

DESCRIPTION: Family characters listed by Miller (1925:94) include: (1) lateral and backward extension of post-auditory prominences; (2) close approximation of maxillopalatines; (3) reduction of cerebellar region; (4) compression and vaulting of beak; (5) elliptical foramen magnum; (6) broadening and shortening of sternum; (7) weakness and openness of furcula; (8) ruggedness of humeral head; (9) elongation and attenuation of ulna and metacarpus; (10) relative weakness of posterior limbs; (11) reduction of trochanter of femur; (12) reduction of tibial crests; (13) columnar character of tarsometatarsus. Additional characters not listed by Miller include (14) skull broad and dorsoventrally flattened; and (15) quadrate with an L-shaped mandibular articulation extending without break from quadratojugal socket to anteromost point of ventral surface.

***Argentavis* new genus**

TYPE SPECIES: *Argentavis magnificens* new species.

DIAGNOSIS: Differs from *Teratornis* L. Miller 1909 by having skull (Fig. 1a, b) (1) broader, more flattened dorsoventrally, with greater posterolateral extension of postauditory prominences; with (2) foramen magnum lying in a plane facing more posteriad, i.e., more vertical; (3) foraminal openings immediately anterolateral to occipital condyle large, but possibly enlarged by breakage (very small in *Teratornis*); (4) occipital condyle as wide as widest portion of foramen magnum (about

Table 1. Measurements (in mm) of *Argentavis magnificens* new genus new species, *Teratornis merriami* L. Miller,[1] and *Gymnogyps californianus* (Shaw) (n = 1).

	Argentavis magnificens	*Teratornis merriami*	*Gymnogyps californianus*
Skull			
Length	435 ± 20	222.0	158.0
Maximum width through postauditory prominences	150 ± 10	86.7	50.0
Top of cranium through ventral tip of occipital condyle	66 ± 5	55.7	45.0
Maximum width of foramen magnum	15.5 ± 1	12.2	11.4
Height of foramen magnum	17.5 ± 1	13.4	12.5
Width of occipital condyle	15.0	9.5	6.1
Height of occipital condyle	11.0	6.1	5.0
Quadrate			
Maximum distance from squamosal articulation to tip of mandibular articulation	66 ± 2	36.7–39.2 38.3	27.8
Anteroposterior ventral length	46 ± 3	24.2–28.5 26.4	18.0
Center of socket for quadratojugal to anterior end of mandibular articulation	53 ± 2	25.5–28.3 26.8	15.3
Humerus			
Length	570 ± 10	310.0–330.0 318.2	271.0
Least width of shaft	49.0	22.9–26.7 24.6	21.0
Depth of shaft at point of least width	35.0	17.6–20.5 19.5	16.0
Coracoid			
Head to internal distal angle	325 (est.) (as preserved, 205)	151.3–163.5 156.5	98.0
Head to medial opening of coracoidal fenestra	125.0	70.1–77.7 74.4	53.2
Maximum width of glenoid facet	31.0	17.9–18.8 18.3	13.4
Dorsal end of glenoid facet to ventral end of procoracoid	78.0	39.1–42.6 40.5	35.7
Tarsometatarsus			
Length	240 (est.) (as preserved, 133)	130.4–145.8 139.8	121.5
Width at distal end of distal foramen	42.0	20.8–23.4 22.0	22.5

[1] Measurements for the skull were taken from specimen No. LACM HCB1381. For the other elements, measurements were taken from five complete specimens of each from the collections in the George C. Page Museum, Natural History Museum of Los Angeles County. This group of measurements is not intended to be definitive for the species, but only to demonstrate its general size.

one-third narrower than foramen magnum in *Teratornis*); (5) transverse ridge connecting the postauditory prominences absent; (6) postauditory prominence with posterolateral corner less angular, not projecting ventral to occipital condyle in posterior view; (7) quadratojugal with quadrate articulation projecting much less sharply ventrad.

Tarsometatarsus (Fig. 4l–m) with (1) center of shaft in anterior view distinctly elevated above those portions of shaft leading to internal and external trochleae, resulting in the distal foramen lying well below the elevation of the center of the shaft (in *Teratornis* the shaft is well rounded in this area, with opening for distal foramen lying at same level as anterior edge of center of shaft); (2) distal foramen of uniform width throughout its length, with outer extensor groove leading to it restricted in width by elevated center of shaft (distal foramen wider proximally than distally in *Teratornis,* with outer extensor groove wide proximally, narrowing significantly at distal foramen); (3) shaft with anterior half at most proximal preserved point quite convex, with medial side extending farthest anteriad (in *Teratornis,* anterior metatarsal groove extends distad to become outer extensor groove, so anterior half of shaft is not convex at any point proximal to distal foramen); (4) shaft appears elliptical in cross section at most proximal point preserved, with long axis of ellipse running anteromedially-posterolaterally (roughly rectangular in *Teratornis,* being wider than deep); (5) shaft edge external to distal foramen more convex.

Differs from *Catharthornis* Miller 1910 by having tarsometatarsus with anterior surface of shaft convex (strongly grooved, or channeled, throughout length in *Cathartornis*).

ETYMOLOGY: Latin, *argentum,* silver; *avis,* feminine, bird. In reference to Argentina, the country of origin.

MEASUREMENTS: For measurements of the holotype see Table 1.

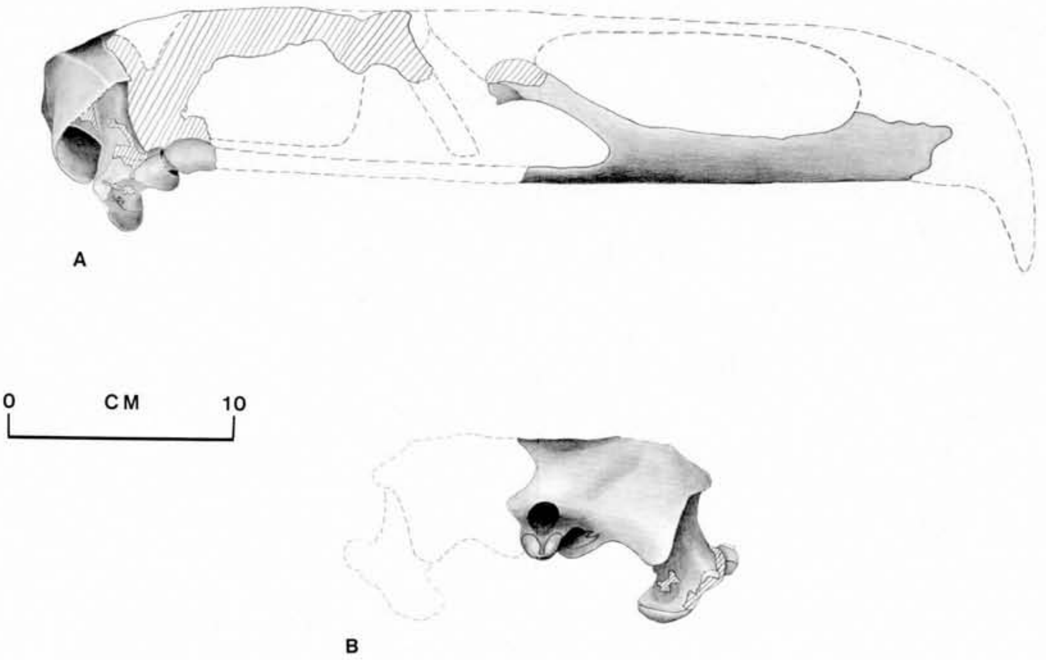

Figure 1. Holotype (Museo de la Plata No. 65-VII-29-49) skull of *Argentavis magnificens* new genus new species in lateral (a) and posterior (b) view. ×0.30. In this and all other figures the hatched areas represent portions of the specimen where the bone has flaked away, but the matrix remains to show form; the dotted lines show estimated outline of bone where missing, based upon corresponding bones of *Teratornis merriami*.

Argentavis magnificens new species

Figures 1, 2a–c, 3, 4

HOLOTYPE: Associated partial skeleton, consisting of portions of skull, right quadrate, humeral end and shaft of right coracoid, left humerus with badly damaged proximal and distal ends, portion of shaft of left(?) ulna, portion of shaft of right radius, distal end of left metacarpal II, midportion of left metacarpal III, shaft of right tibiotarsus, shaft of right tarsometatarsus. Original in the División Paleontología Vertebrados del Museo de La Plata, No. 65-VII-29-49; cast in Natural History Museum of Los Angeles County, LACM 120074. Collected by Rosendo Pascual and Eduardo Tonni.

TYPE LOCALITY: Salinas Grandes de Hidalgo, Departamento Atreucó, La Pampa Province, Argentina. Located about 15 km south of the Hidalgo station on the railroad connecting Carhué (Buenos Aires Province) with Doblas (La Pampa Province), approximately 37°14′S, 63°36′W; see Figure 5.

HORIZON AND AGE: Epecuén Formation (fide Pascual 1961) (lowest level outcropping at locality). Huayquerian (late Miocene).

DIAGNOSIS: As for genus. For measurements see Table 1.

ETYMOLOGY: Latin, *magnificens*, magnificent.

DESCRIPTION: All of the bones have been severely fractured, but, except for the skull, crushing has been minimal. The fracture lines have been omitted from the illustrations. In some places the bone has flaked away, leaving only a replica in matrix to indicate its general form. Where this has happened in areas without diagnostic characters, the illustrations were prepared as if the bone were still present. Hatching indicates where bone has broken away in diagnostic areas, leaving only the general form. Unfortunately, all the bones of the postcranial skeleton lack their most diagnostic portions. Were it not for the partial skull and quadrate, the specimen would have to be considered indeterminate; but these two elements provide strong evidence that relates *Argentavis* to *Teratornis*.

The quadrate (Fig. 2a–c) of *Argentavis* differs from that of *Teratornis* by having (1) quadratojugal socket positioned farther from main body of quadrate, i.e., with short leg of L-shape proportionately longer, giving appearance of having a "neck;" (2) mandibular articulation extending farther anteroventrad, but not as far anteriad proportionately, giving greater degree of curvature to ventral edge in medial view; (3) pterygoid articulation positioned more laterally; (4) squamosal articulation with medial portion hemispheric, mounted on columnar-like structure (medial portion elongated, positioned on more massive extension of main body of quadrate in *Teratornis*); (5) mandibular articulation with anterior one-half of medial portion, i.e., its long leg, proportionately much larger, lying at less of an angle to horizontal.

The coracoid of *Argentavis* (Fig. 4a–d) is characterized by having (1) shaft laterally compressed at humeral end, nearly flat anterior to glenoid facet (not compressed, and well rounded anterior to glenoid facet in *Teratornis*); (2) procoracoid reduced, with ventral margin lying at about 45 degrees to main axis of shaft (not reduced, with ventral margin straight and lying at 90 degrees to main axis of shaft in *Teratornis*); (3) glenoid facet deeply concave in lateral view, with deepest point lying just ventral to horizontal midline of facet (slightly concave in lateral view, with deepest point lying near ventral end in *Teratornis*); (4) glenoid facet in posterior view with medial edge roughly vertical and in line with coracoidal fenestra, and parallel to main axis of shaft (sloping significantly mediad from dorsal to ventral points in posterior view, not in line with

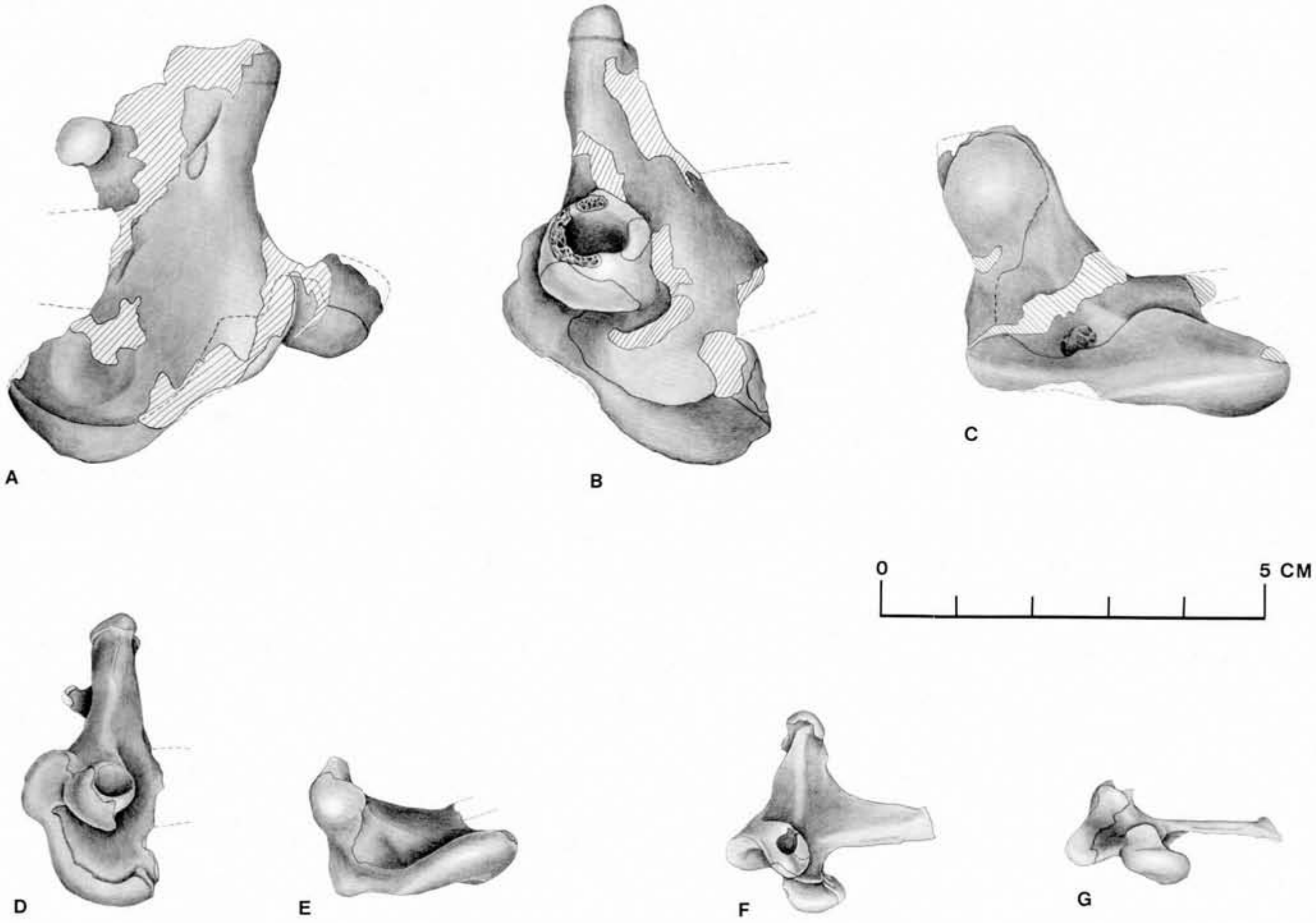

Figure 2. Holotype (Museo de la Plata No. 65-VII-29-49) right quadrate of *Argentavis magnificens* new genus new species in posterolateral (a), lateral (b), and ventral (c) view; quadrate of *Teratornis merriami* L. Miller (LACM HCB747) in lateral (d) and ventral (e) view; quadrate of *Gymnogyps californianus* (Shaw) (LACM Bi1800) in lateral (f) and ventral (g) view. All ×1.

coracoidal fenestra or main axis of shaft in *Teratornis*); (5) coracoidal fenestra lying much nearer procoracoid, and opening mediad more posteriorly; (6) ridge leading ventrad from procoracoid toward internal distal angle small, but distinct (absent in *Teratornis*).

The humerus of *Argentavis* (Fig. 3a–b) differs from that of *Teratornis* by having (1) shaft in anterior view with proximal two-thirds relatively straighter and distal one-third curving more sharply dorsad; (2) shaft in dorsal view appearing more strongly sigmoid; (3) external tricipital groove appearing to extend proximad to ectepicondylar prominence, which is broken away (does not extend proximad to ectepicondylar prominence in *Teratornis*); (4) deltoid crest with very pronounced knob, the distal portion of which is broken away (similar, but with knob less elevated above and less sharply demarcated from shaft proximally in *Teratornis*); (5) shaft slightly less but still deeply convex between deltoid crest and bicipital crest.

The preserved portion of the ulna of *Argentavis* (Fig. 4i) has no diagnostic characters, displaying only three papillae of the secondaries spaced about 30 mm apart (spaced about 15 to 18 mm apart in *Teratornis merriami*).

The carpometacarpus of *Argentavis* (Fig. 4e–h) differs from that of *Teratornis* by having metacarpal II with (1) tendinal groove deeper, bordered by more pronounced ridges, and lying more anteriorly on external side of shaft; (2) shaft with posterior half more rounded, with a small ridge lying on posterior side and extending a short distance proximad to most proximal point preserved (ridge absent in *Teratornis*); (3) distal metacarpal symphysis lies closer to center of shaft proximally; (4) facet for digit II with that portion preserved having anterior end extending farther posteriad at a greater angle. Metacarpal III has (1) shaft more triangular in cross section; (2) anterior surface more excavated, bordered externally by more pronounced ridge).

The tibiotarsus of *Argentavis* (Fig. 4j–k) lacks any diagnostic characters, but can be seen to differ from that of *Teratornis* by having (1) shaft slightly curved in anterior view, although some curvature seen in Figure 4j–k may be a result of breakage (essentially straight in *Teratornis*); (2) fibular crest much less developed, although this may be a result of breakage; (3) tendinal groove with proximal end more symmetrical and lying near center of shaft rather than near internal edge of shaft.

AGE AND ASSOCIATED FAUNA

The holotype of *Argentavis magnificens* was collected from the brownish to reddish terrestrial sediments of the late Miocene Epecuén Formation (fide Pascual 1961). This formation

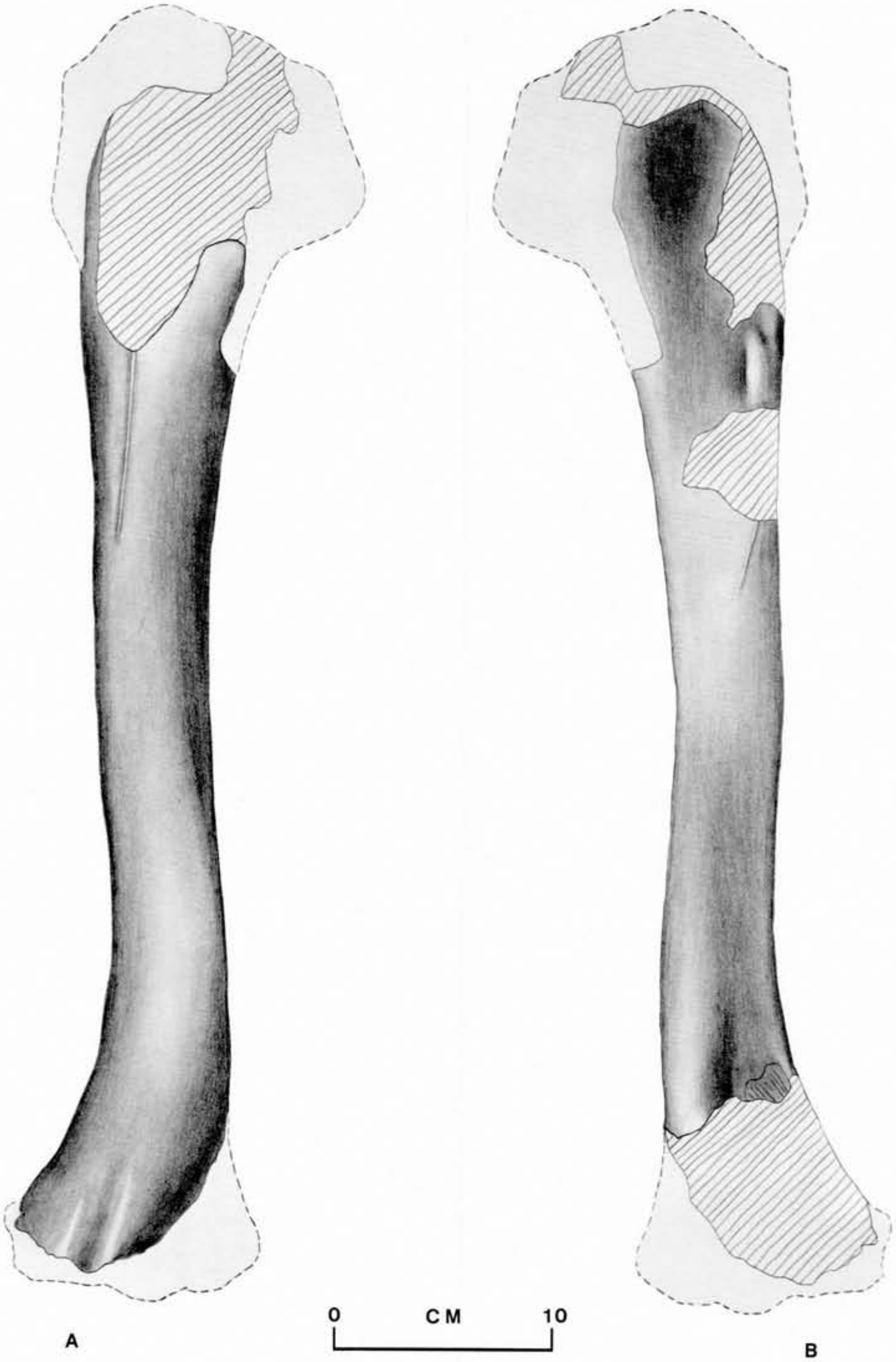

Figure 3. **Holotype** (Museo de la Plata No. 65-VII-29-49) left humerus of *Argentavis magnificens* new genus new species in **anconal** (a) and palmar (b) view. ×0.30.

is composed primarily of fine sand with minor amounts of silt and rare lenses of clay. Irregular thicknesses of caliche-like concretions occur at several levels; isolated concretions may also occur.

The late Miocene age assignment of the Epecuén Formation is based on the following mammalian fauna reported for the deposits of Salinas Grandes de Hidalgo by Zetti (1972): Order Marsupialia, Family Borhyaenidae: *Borhyaenidium musteloides* Pascual and Bocchino, *Thylacosmilus* aff. *atrox* Riggs; Order Carnivora, Family Procyonidae: *Cyonasua brevirostris* Moreno and Mercerat; Order Notoungulata, Family Toxodontidae: *Pisanodon* n. sp.; Family Hegetotheriidae: *Hemihegetotherium* n. sp., *Paedotherium borrelloi* Zetti; Order Litopterna, Family Macraucheniidae: ?*Promacrauchenia* sp.; Order Edentata, Family Mylodontidae: *Elassotherium altirostre* Cabrera; Family Dasypodidae: *Proeuphractus* sp., *Macroeuphractus* sp.; Family Glyptodontidae: Sclerocalyptinae gen. et sp. indet.; Order Rodentia, Family Caviidae: *Orthomyctera*

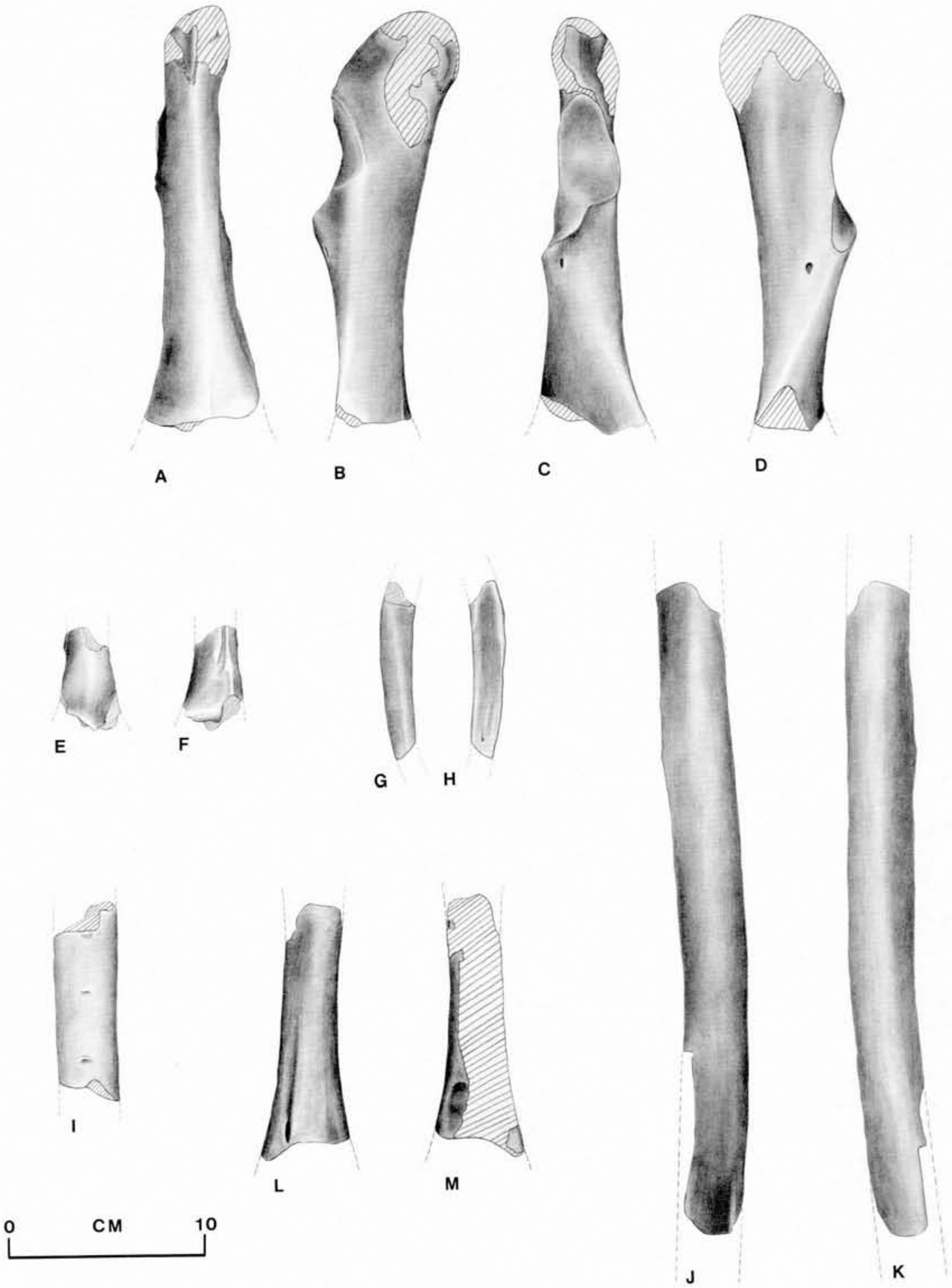

Figure 4. Holotype (Museo de la Plata No. 65-VII-29-49) of *Argentavis magnificens* new genus new species: right coracoid in anterior (a), lateral (b), posterior (c), and medial (d) view; distal end of left metacarpal II in internal (e) and external (f) view; medial portion of left metacarpal III in lateral (g) and medial (h) view; portion of shaft of left(?) ulna in anconal (i) view; shaft of right tibiotarsus in anterior (j) and posterior (k) view; shaft of right tarsometatarsus in anterior (l) and posterior (m) view. ×0.30.

sp., *Paleocavia* sp.; Family Hydrochoeridae: ?Protohydrochoerinae gen. et sp. indet.; Family Chinchillidae: *Lagostomopsis* sp.; Family Octodontidae: *Phtoramys* sp., *Pseudoplataeomys* sp.; Family Echimyidae: ?*Eumysops* sp.

This assemblage of mammalian taxa is characteristic of the Huayquerian (*sensu* Pascual et al. 1965), a South American land mammal age conventionally referred to the late Miocene (Marshall et al. 1979). In addition to *Argentavis magnificens* and the mammalian fauna, reptiles and other birds are known from the deposits, but have yet to be described.

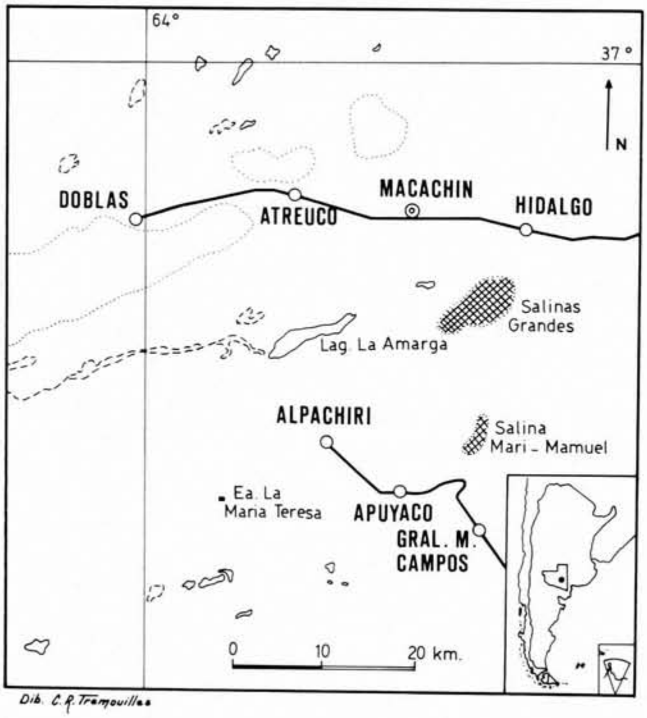

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Figure 5. Map showing location of type locality, Salinas Grandes, in Argentina.

DISCUSSION

The similarities of the skull and quadrate of *Argentavis* to those of *Teratornis* are very striking when characters of these two genera are contrasted with those of genera of the other accipitriform families. Although the unique structure of the teratorn skull has been commented on since its description (Miller 1909), there has been no attempt to analyze it as there has been for its postcranial skeleton (Fisher 1945). The studies now in progress on *Teratornis merriami* will attempt to fill this void. A few preliminary comments about functional morphology that apply to both *Argentavis* and *Teratornis* are presented here.

Teratornis appears to be more specialized than *Argentavis*, e.g., by having the postauditory prominences ending in a more angular corner that projects ventral to the occipital condyle and a prominent transverse ridge connecting the postauditory prominences. *Teratornis* also has the posterior portion of the skull much more rounded, in both lateral and posterior view (for illustrations of *T. merriami* see Miller 1909, 1925; Jollie 1978). It is not possible to make additional cranial comparisons because of the damaged nature of the holotype skull of *Argentavis magnificens*.

The posterior extension of the postauditory prominences is an adaptation to increase the gape of the mouth by moving the hinge line of the jaw posteriad. In both *Argentavis* and *Teratornis* the quadrate articulates with the squamosal posterior to the occipital condyle, giving the maximum possible gape without actually having the squamosal lying farther posteriad than the parietal or supraoccipital.

The articulation of the quadrate with the squamosal is such that, when the ventral end is swung through its arc, it moves posterolaterally at an angle of about 45 degrees to the long axis of the skull. This contrasts with the condition found in other accipitriform families where the quadrate movement is almost parallel to the long axis of the skull, and is far more restricted. By rotating the quadrate so that the ventral end moves laterad as much as it moves posteriad, pressure is exerted on the articular of the lower jaw, forcing the rami of the lower jaws apart posteriorly. A similar, but less developed, condition is found in pelicans (Pelecaniformes: Pelecanidae), and the pelican quadrate bears a strong superficial resemblance to the teratorn quadrate. The Frigatebird, *Fregata magnificens* (Pelecaniformes: Fregatidae), and albatrosses (Procellariidae: Diomedeidae) also have a similar condition.

As illustrated by *Gymnogyps* (Fig. 2f–g), in the family Vulturidae the mandibular articulation is not "L-shaped" or continuous, and the two portions do not lie perpendicular to each other. All genera of vulturids have a distinct shelf on the medial side of the anterior portion of the mandibular articulation, a character limited to that family within the Accipitriformes. The lateral component of the articular movement on the quadrate, and of the quadrate on the squamosal, in *Gymnogyps* and other vulturids is minimal.

In the teratorn quadrate, the quadratojugal socket is much less restrictive than in vulturids, an adaptation that assists the lateral movement of the quadrate. A similar condition exists in frigatebirds and albatrosses; in the pelicans there is no socket present, only a flat or convex articular surface.

The lower jaw of *Argentavis* is unknown, which is perhaps to be expected if it resembled that of *Teratornis*. The lower jaw of *Teratornis merriami* is very weak, as noted by Howard (1950), and even at Rancho La Brea no complete specimens are known; the portion immediately anterior to the mandibular foramen was apparently such a thin sheet of bone that it was never preserved, or it was lost in collection and preparation. This character is also an adaptation for lateral movement of the posterior portion of the lower jaw; it provides a weak spot where the jaw can flex without having a weak symphysis. This condition is also present in frigatebirds and albatrosses. The exact function of this character complex in feeding remains to be worked out, but it appears very unlikely that teratorns fed in a manner similar to any other accipitriform.

A comparison of the measurements of *Argentavis magnificens* and *Teratornis merriami* reveals that the former is almost twice the size of the latter in almost all measurements. If we were to assume that it is reasonable to extrapolate directly from the estimated size of *T. merriami* (isometric scaling), we could say that *A. magnificens* had a wingspan of 7 to 7.6 m, a height of 1.5 m, and a weight of 120 kg. Of course, there is the possibility that isometric scaling may not be applicable in this case. Also, because the size of *T. merriami* was calculated with the consideration in mind that it was a condor-like bird, its estimated wingspan may be quite erroneous; and the estimate may as well be too small as too large. The estimate of the height and the new weight estimate of *T. merriami* are probably much more accurate. In spite of these qualifications, *A. magnificens* is certainly the largest flying bird known to have existed.

The question as to how such a tremendously large bird like *Argentavis magnificens* could fly remains unanswered. It is often believed that very large flying birds must depend on wind currents to become airborne and remain aloft, and that "the maximum size attainable by flying birds is limited by surface-volume ratio and the speed of flight" (Storer 1971:152). Or, "The larger the bird, the faster it must fly to stay airborne" (Pettingill 1970:2). As noted above, however, Fisher (1945) suggested that *T. merriami* was capable of flapping flight, possibly similar to that of herons and pelicans, both of which may fly at speeds considerably slower than that observed for many smaller species. Storer (1971:153) commented that "Under present conditions, the larger albatrosses, pelicans, storks, swans, condors, turkeys, and bustards must represent about the largest size to which flying birds can evolve." While it is certainly true that environmental conditions in La Pampa Province of Argentina were very different in the Huayquerian than they are today, it is questionable whether the mechanics of avian flight have changed. Rather, there is a greater probability that our understanding of avian flight is still very incomplete.

The presence of a teratorn in South America should not be considered too surprising. Campbell (1979), in a study of the late Pleistocene avifauna of the Talara Tar Seeps of northwestern Peru, described a new species of *Gymnogyps* and a new genus and species of large eagle, *Amplibuteo hibbardi*; both genera were previously known only from North America (*G. amplus* and *G. californianus*; *Amplibuteo* (=*Morphnus*) *woodwardi*). Many Recent species previously reported as fossils only from North America were also reported from the Talara Tar Seeps. Earlier, Campbell (1976) reported an indeterminate fragmentary vulturid tarsometatarsus from La Carolina, Ecuador, that differed markedly from the three genera of condors later reported from the Talara Tar Seeps. A recent comparison of this specimen with tarsometatarsi of *T. merriami* from Rancho La Brea, California, shows that although it is not referable to *Teratornis merriami,* there is a very good possibility that it is from a different species of *Teratornis*. As collections of avian fossils, particularly those from South America, increase, we can expect to find many more examples of what have been considered North American groups appearing in South America, and vice versa (e.g., see Campbell this vol.).

Although there is a good possibility that the Teratornithidae should not be placed within the Accipitriformes, it is prudent at the present time to leave it there pending completion of more detailed studies. It can be stated that there are almost no points of similarity between the cranial osteology of teratorns and that of the members of the Falconidae, Accipitridae, Serpentariidae, or Vulturidae. And, although there are similarities between the postcranial skeleton of teratorns and those of the other families of Accipitriformes, there are many more striking differences.

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MIDDLE PLIOCENE RAILS FROM WESTERN MONGOLIA

By E.N. Kurochkin[1]

ABSTRACT: The fossil remains of three new species of rails from three Middle Pliocene localities in the Ich Nuuryn Töchöm of Western Mongolia are described. These include *Palaeoaramides tugarinovi* new species, *Rallus risillus* new species, and *Crex zazhigini* new species. Rails are practically absent from Ich Nuuryn Töchöm today, and the presence of three species of rails in Western Mongolia during the Middle Pliocene indicates that there has been a change in the climatic and ecological conditions found there since that time.

Soviet and Mongolian paleontologists and geologists have discovered many fossil localities (Chirgis Nuur II, Chono Hariagh, Dzavchan, "point 1080 m" in Ŝargyn Gov' Desert, Javor I, and others) in the western part of the Mongolian People's Republic (MPR) in the Ich Nuuryn Töchöm (The Great Lakes Depression) in the past few years. These workers have recovered numerous fragmentary remains of Middle Pliocene vertebrates.

The fossil localities are located on the eastern border of the Töchöm, and run in a line from north to south for almost 400 km. The vertebrate remains occur in the Middle Pliocene (Devjatkin and Zhegallo 1974) sand and aleurite sediments of the lacustrine and nearshore-lacustrine facies. These deposits are stratigraphically apportioned by Devjatkin (1970) to the Chirgis Nuur series.

The majority of the vertebrate remains from these localities are mammalian, but fossils of fish, reptiles, amphibians, and ostracods, as well as a considerable number of birds were also collected. The birds are represented by approximately 200 fragments of postcranial bones, as well as by numerous ratite egg shell fragments. The total number of birds identified from the avifauna include 55 species belonging to 11 orders and 15 families (Phalacrocoracidae, Ardeidae, Ciconiidae, Anatidae, Phasianidae, Gruidae, Ergilornithidae, Rallidae, Scolopacidae, Phalaropodidae, Pteroclidae, Strigidae, Psittacidae, Corvidae, and Turdidae). Water birds and shorebirds are predominant in the collection, and the waterfowl are most numerous, with 14 species. Part of the paleornithological material has been described previously (Kurochkin 1971, 1976), and a description of all of the material is now being prepared for publication as a monograph. The present paper contains the description of the rallid remains from three localities: "point 1080 m," located in the central region of the Ŝargyn Gov' Desert in the south of the Töchöm; "Chono Hariagh," located on the northern shore of the river with the same name between Chovd Dalaj Nuur and Char Nuur Lakes; and "Chirgis Nuur II," located on the northern shore of Chirgis Nuur Lake.

SYSTEMATICS

Order Ralliformes

Suborder Ralli

Family Rallidae

Subfamily Rallinae

Genus *Palaeoaramides* Lambrecht 1933

***Palaeoaramides tugarinovi* new species**

Figures 1, 5a

HOLOTYPE: Distal end of right humerus, No. 2614-121, Collection of the Paleontological Institute of the USSR Academy of Sciences (PIN).

LOCALITY: "point 1080 m" in Ŝargyn Gov', the Gov' Altaj ajmak, MPR; Middle Pliocene.

DIAGNOSIS: Humerus with (1) sulcus anconeus externus shallow; (2) processus supracondylus externus well developed, forming prominent transverse step; (3) attachment of M. pronator brevis distinctly separated.

MEASUREMENTS (in mm): Greatest width of distal end 5.5; anteroposterior depth of condylus radialis 3.3; anteroposterior depth of condylus ulnaris 1.9; distance from top of facies ligamenti interni to distal edge of condylus ulnaris 3.2; least depth of distalmost portion 2.1.

ETYMOLOGY: This species is named in honor of the memory of Professor A.Y. Tugarinov.

COMPARISON: Four species of *Palaeoaramides* are known from the Lower (Aquitanian) and Upper Miocene of Europe (Olson 1977). Three of these have been described and compared on the basis of tibiotarsi and tarsometatarsi, but *P. beaumontii* (Milne-Edwards 1869) was described from a humerus from the Upper Miocene (Helvetian) of France (Sansan locality in the Gers Department). Illustrations of the humerus of *P. beaumontii* are given in the Atlas by Milne-Edwards (1869–1871), as well as by Cracraft (1973) in stereophotographs. These illustrations proved to be sufficient for the determination and comparison of the rallid humerus from Ŝargyn Gov'.

The humerus of *P. tugarinovi* new species and *P. beau-*

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Contrib. Sci. Natur. Hist. Mus. Los Angeles County. 1980. **330:**69–73.

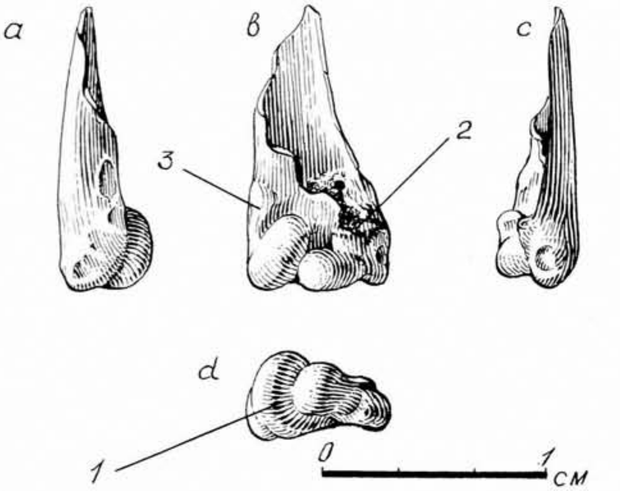

Figure 1. *Palaeoaramides tugarinovi* new species, holotype, distal end of right humerus, No. 2614-121 PIN; locality "point 1080 m," Ŝargyn Gov', Mongolia, in dorsal (a), palmar (b), ventral (c), and distal (d) view. 1, incisura intercondylaris; 2, processus supracondylus externus; 3, eminentia M. pronator brevis.

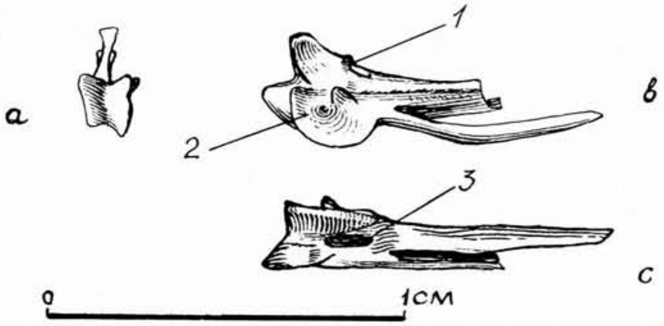

Figure 3. *Rallus risillus* new species, holotype, proximal portion of left carpometacarpus, No. 2614-100 PIN; locality "point 1080 m" in Ŝargyn Gov', Mongolia, in proximal (a), internal (b), and posterior (c) view. 1, facies articularis pollicis; 2, fossa carpalis interna; 3, fossa carpalis posterior.

montii are very similar in the structure and disposition of both condyles, as well as in the structure of the epicondylus ulnaris (or processus flexoris). The latter is notably elongated distally and salient on the internal surface of the specimen. The facies ligamenti interni is similar in both. It is oval in outline, extends high externally, with its plane directed laterad and dorsad. The impression of M. brachialis inferioris also has the same outline and dimensions in both. The condylus ulnaris and epicondylus ulnaris in both species are separated by a distinct groove that is very characteristic of the genus.

Structural differences in the distal end of the humeri between *P. tugarinovi* and *P. beaumontii* were presented in the diagnosis. The sulcus anconeus externus is notably smaller in *P. tugarinovi* than in *P. beaumontii.* The processus supracondylus externus and eminentia M. pronator brevis are more developed in *P. tugarinovi,* as compared with *P. beaumontii. Palaeoaramides tugarinovi* was smaller than *P. beaumontii* (width of distal epiphysis 6.2; anteroposterior depth of the condylus radialis 3.6; anteroposterior depth of the condylus ulnaris 1.9 (from Cracraft 1973).

DISCUSSION: Cracraft (1973) pointed out the general similarity of *Palaeoaramides* and Recent *Rallus* Linnaeus. This position is confirmed with this specimen. Of all modern species of the Rallinae, *Palaeoaramides* is most similar to *Rallus,* as concluded from the general proportions of the condyles, from the outline and dimensions of the fossa olecrani, from the curvature of the distal part of the diaphysis, and from the outline of the facies ligamenti interni. But these two genera can well be distinguished by the structure of the epicondylus ulnaris, which is narrower and elongated internally in *Palaeoaramides* and weakened in *Rallus.* In *Palaeoaramides* the visible depression lies between the epicondylus ulnaris and condylus ulnaris. *Rallus* does not have such a depression, which results from the distal prolongation of the ventral edge of the condylus ulnaris. The impression of M. brachialis inferioris in *Palaeoaramides* is shallower and broader than in *Rallus.*

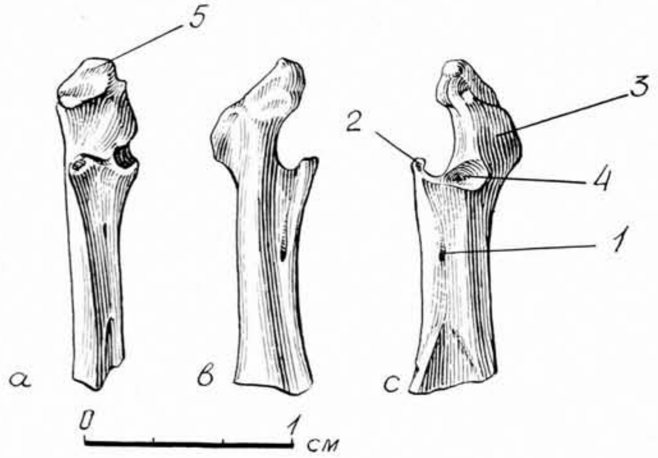

Figure 2. Cf. *Palaeoaramides tugarinovi,* referred humeral end of right coracoid, No. 3222-55 PIN; locality Chirgis Nuur II on the shore of Chirgis Nuur Lake, Mongolia, in internal (a), anterior (b), and posterior (c) view. 1, foramen supracoracoideum; 2, processus procoracoideus; 3, facies glenoidalis; 4, cotyla scapularis; 5, tuber brachialis.

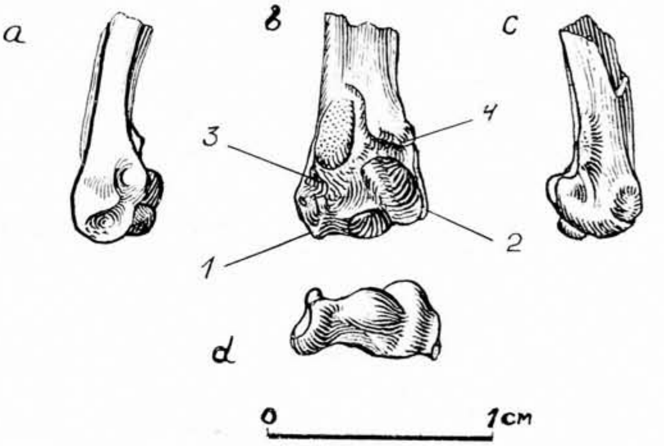

Figure 4. *Crex zazhigini* new species, holotype, distal end of left humerus, No. 2614-90 PIN; locality Chono Hariagh in Chovd ajmak, Mongolia, in ventral (a), palmar (b), dorsal (c), and distal (d) view. 1, entepicondylus; 2, ectepicondylus; 3, processus supracondylus externus; 4, transversal line tuberosity.

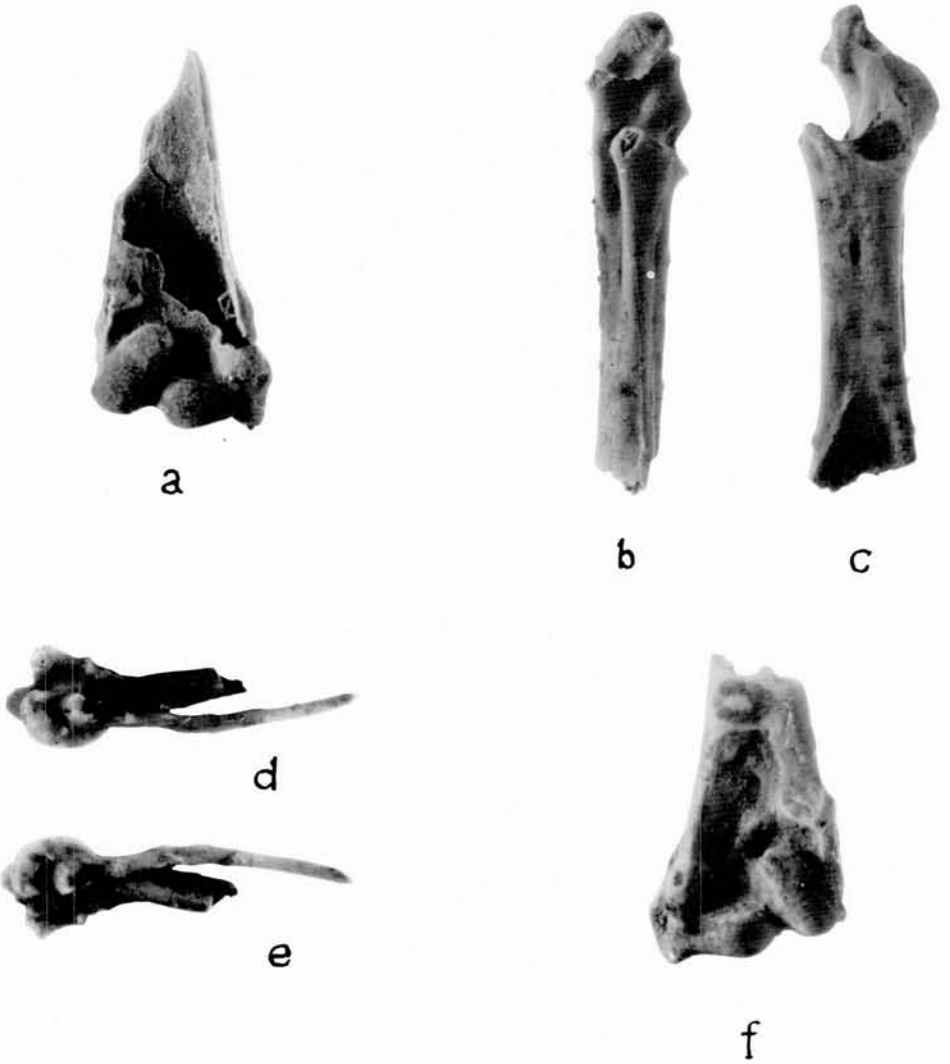

Figure 5. a. *Palaeoaramides tugarinovi* new species, holotype, No. 2614-121 PIN, palmar view; b–c. cf. *Palaeoaramides tugarinovi,* referred coracoid, No. 3222-55 PIN, in internal (b) and posterior (c) view; d–e. *Rallus risillus* new species, holotype, No. 2614-100 PIN, in internal (d) and external (e) view; f. *Crex zazhigini* new species, holotype, No. 2614-90 PIN, palmar view. (all ×4).

cf. *Palaeoaramides tugarinovi*

Figure 2, 5b, c

MATERIAL: Humeral end of left coracoid, No. 3222-55 (PIN).

LOCALITY: Chirgis Nuur II, MPR; Middle Pliocene.

DISCUSSION: The coracoids of the four described fossil species of *Palaeoaramides* remain unknown. The specimen here referred to *P. tugarinovi* has its most pronounced structural similarity with *Rallus,* but it still differs in certain morphological characters from that genus. The similarities include (1) the identical structure of the dorsal portion of the diaphysis, with the same localization and form for foramen supracoracoideum; (2) the same degree of development and form for processus procoracoideus; (3) the same form for cotyla scapularis; and (4) the same proportions of the acrocoracoideum. However, the details of the acrocoracoid are different: (1) The facet on the external side of the acrocoracoid is narrower and more extended in *P. tugarinovi.* (2) This is also the case with the facies glenoidalis, which is more extended distally over the level of processus procoracoideus in *P. tugarinovi,* whereas in *Rallus aquaticus* Linnaeus the facies glenoidalis and processus procoracoideus are positioned at one transverse level. (3) The tuber brachialis in *P. tugarinovi* is smaller and more extended along the diagonal. It is more elongated internally and projects somewhat over the foramen triosseum, as compared with that of *R. aquaticus.*

This specimen is referred to *P. tugarinovi* on the basis of a unique combination of morphological characters that occur in the coracoid and humerus of modern rails. This conclusion results from similar comparisons, taking into account the appropriate relative measurements of the holotype of *P. tugarinovi* and the referred coracoid.

MEASUREMENTS (in mm): Transverse width of diaphysis 2.4; length of dorsal epiphysis (from ventral edge of cotyla scapularis) 5.6; width of facies articularis scapularis 2.4. On the basis of measurements, this specimen appears to have come from a bird between the size of *R. aquaticus* and *R. longirostris* Boddaert, being slightly closer to the former. This is also true for the holotype humerus of *P. tugarinovi.*

Rallus Linnaeus 1758

Rallus risillus **new species**

Figures 3, 5d–e

HOLOTYPE: Proximal end of left carpometacarpus, No. 2614-100, Collection of the Paleontological Institute of the USSR Academy of Sciences.

LOCALITY: "point 1080 m" in the central region of the Šargyn Gov' Desert, the Gov' Altaj ajmak, MPR; Middle Pliocene.

DIAGNOSIS: Carpometacarpus with (1) facies articularis pollicis appearing as small step, not sharply set off from metacarpal II; (2) fossa carpalis posterior lengthened and shallow; (3) fossa carpalis interna small; (4) anteroproximal end of trochlea radialis lying on same longitudinal axis as apophysis pisiformis; (5) size very small.

MEASUREMENTS (in mm): Transverse width of trochlea carpalis 1.5; anteroposterior width of trochlea carpalis (with processus metacarpalis I) 4.0.

ETYMOLOGY: From Latin, *risillus,* masculine, very small.

COMPARISON: The fossil rails are one of the best known groups of fossil birds (Feduccia 1968; Olson 1973, 1974, 1977). Unfortunately, no carpometacarpi of described fossil rails are available for comparison with *Rallus risillus*. We compared it with Recent *R. elegans* Audubon, *R. longirostris, R. aquaticus,* and *R. limicola* Vieillot. *Rallus risillus* differs from these species in the details of the carpometacarpus listed in the diagnosis. Size is a very important character of *R. risillus,* it being 1.5 times smaller than the American *R. limicola,* the smallest modern representative of the genus. Measurements (in mm) of the carpometacarpus of the four species of Recent rails are as follows. Transverse width of trochlea carpalis: *R. elegans* 3.1; *R. longirostris* 2.8; *R. aquaticus* 2.2; *R. limicola* 2.1. Anteroposterior width of trochlea carpalis (with processus metacarpalis I): *R. elegans* 7.1; *R. longirostris* 6.2; *R. aquaticus* 4.6; *R. limicola* 4.3.

In Recent *Rallus* the articulating surface of facies articularis pollicis is widened on each side, with the surface of metacarpal II sharply set off at almost a right angle to it. This contrasts with the narrow surface in *R. risillus* that is not set off from the surface of metacarpal II by a sharp angle. But a small *R. limicola* has this angle somewhat blunted. The fossa carpalis posterior, located on the interior side of trochlea radialis, is much shorter and deeper in Recent *Rallus* than in *R. risillus*. Only in *R. aquaticus* is it slightly elongated, tending toward that of *R. risillus*. The fossa carpalis interior, on the interior face of trochlea carpalis, of modern *Rallus* is deeper, larger, and farther from the apophysis pisiformis than that of *R. risillus*. In *R. risillus* the anteroproximal angle of the trochlea carpalis lies on the same longitudinal axis as the apophysis pisiformis, approximately the same position found in *R. aquaticus*. The three other species of *Rallus* have this angle shifted more caudad.

REMARKS: The comparative material of the modern Rallinae used for the description of *R. risillus* was naturally insufficient. Most of the modern tropical genera of this subfamily were not represented in the comparative series. However, I am quite certain that *R. risillus* is closest to the genera *Rallus* and *Porzana* Vieillot. *Rallus risillus* resembles *Porzana,* as indicated by comparison with *P. porzana* Linnaeus, *P. parva* (Scopoli), *P. carolina* Linnaeus, and *P. flaviventer* (Boddaert), by having (1) the same structure of metacarpal II, which also rises gradually to the facies articularis pollicis, (2) relatively similar dimensions, and (3) the fossae carpalis posterior et interior similar in form. However, the relative dimensions of metacarpal I and metacarpal II, and their position with respect to the carpal trochlea, indicate that *R. risillus* should be referred to *Rallus*. In addition, the groove running between metacarpal I and metacarpal II begins at approximately the same position in modern *Rallus* as it does in *R. risillus,* but in *Rallus* it begins notably more proximal than in *Porzana*. The proximal articulating surface of trochlea carpalis is divided on its sides in modern *Rallus,* as in *R. risillus,* and it is relatively wider than in *Porzana*.

Crex Bechstein 1803

Crex zazhigini **new species**

Figures 4, 5f

HOLOTYPE: Distal end of left humerus, No. 2614-90, Collection of the Paleontological Institute of the USSR Academy of Sciences.

LOCALITY: Chono Hariagh, on the northern shore of the Chono Hariagh River in Ich Nuuryn Töchöm, Chovd ajmak, MPR; Middle Pliocene.

DIAGNOSIS: Humerus with (1) impression of M. brachialis inferioris deep and clearly outlined; (2) ectepicondylus shortened; (3) entepicondylus expanded and protruding externad; (4) processus supracondylus externus obtuse and broad; (5) transversal line tuberosity lying proximal from processus supracondylus externus extends across approximately one-third of the shaft at that point.

MEASUREMENTS (in mm): Greatest distal width 6.2; anteroposterior depth of condylus radialis 3.1; anteroposterior depth of condylus ulnaris 1.8.

COMPARISON: *Crex zazhigini* closely resembles Recent *C. crex* (Linnaeus), but differs by having (1) impression of M. brachialis inferioris deep, with clearly marked borders (shallower, without clearly marked borders in *C. crex*); (2) entepicondylus elongated and produced (shortened and not produced in *C. crex*); (3) ectepicondylus shortened (elongated and narrow in *C. crex*); (4) processus supracondylus forming step, widened and blunted medially (pointed in *C. crex*); (5) transversal line tuberosity extending across one-third of the shaft, ending internally at impression of M. brachialis inferioris, and externally at edge of shaft (that tuberosity is lower and narrower in *C. crex*); (6) somewhat larger size (transverse width of distal end of humerus in *C. crex,* 5.3 to 5.5 mm). This is the first record of the genus *Crex* from Neogene deposits.

ETYMOLOGY: This species is named in honor of paleomammalogist V.S. Zazhigin in recognition of his contributions to collecting of Neogene birds in Mongolia.

CONCLUSIONS

Porzana pusilla (Pallas) is the only rail inhabiting western Mongolia today. The presence of several specimens of species of the subfamily Rallinae in upper Middle Pliocene deposits of the Ich Nuuryn Töchöm indicates that the ecological and climatic conditions, and the zoogeographical character, of this region may have been quite different than now. It appears that at the end of the Middle Pliocene the climate of Western Mongolia was not as continental, with milder winters than occur there today. The lakes were probably not as salty, and their shores and the valleys of rivers and streams were covered with rich grass and bush vegetation. Additional evidence of such an environment are the large numbers of waterfowl and gallinaceous birds found in the same deposits.

ACKNOWLEDGMENTS

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A NEW GOOSE FROM THE LATE PLIOCENE OF NEBRASKA WITH NOTES ON VARIABILITY AND PROPORTIONS IN SOME RECENT GEESE

By Larry D. Martin[1] and Robert M. Mengel[2]

ABSTRACT: A nearly complete but moderately crushed skeleton of a late Pliocene (Blancan) goose from the Broadwater Local Fauna of western Nebraska is described and named as *Anser thompsoni* new species. This rather large goose was larger than Recent *Anser caerulescens* (Linnaeus) and smaller than the larger races of Recent *Branta canadensis* (Linnaeus). Particularly distinctive characters include a relatively short bill and a relatively very small furcula. The wing resembled *Anser caerulescens* and *Anser rossii* Cassin in its relatively long ulna. The leg was relatively short as in Recent *Anser albifrons* (Scopoli) and *Branta canadensis*.

Among Hildegarde Howard's many contributions to avian paleontology is her excellent review (1964) of the fossil anseriforms, in which she lucidly considered the strengths and weaknesses of the fossil record of waterfowl and summarized all that was then known. This has been helpfully supplemented by Woolfenden's (1961) thorough study of the qualitative osteology of modern anseriforms.

We have recently begun to study the fossil birds of the Blancan Broadwater Local Fauna of western Nebraska. Most of these are water birds, including a remarkably complete skeleton of a goose that appears to represent a new species of the widespread Holarctic genus *Anser* Brisson.

The completeness of this specimen provided the rare opportunity for a fairly accurate reconstruction of the body proportions of a fossil species. Comparing these with those of Recent geese, however, posed problems. Although Verheyen (1955a, 1955b) has extensively surveyed the rather variable proportions of Recent geese, his sample sizes (one or two, rarely up to four specimens per species) provide little indication of the limits and nature of variation. For comparative purposes we have therefore been obliged to undertake a limited analysis of the relevant aspects of variation in several Recent geese presently represented by major populations in interior North America.

The description of this unusually complete fossil seemed especially appropriate for the present volume in recognition of Howard's long interest in and study of fossil waterfowl and in appreciation of her often stated and intelligently tempered concern (e.g., Howard 1964:235–237) about the problems posed in study of often fragmentary individual specimens.

Only two Blancan local faunas have extensively studied avifaunas: the Rexroad Local Fauna (*sensu lato*) and the Hagerman Local Fauna. Feduccia (1975) has summarized the information pertaining to birds for these two faunas. Other Blancan sites are probably also rich in bird material; this is certainly true of the Broadwater Local Fauna (for correlation chart see Schultz and Martin 1977), which is one of the least studied.

In addition to the birds, the Broadwater Local Fauna has a large mammalian component (list modified from Schultz and Stout 1948:563–564): *Sorex* sp. (shrew), *Paramylodon* sp. (ground sloth), *Megalonyx* sp. (ground sloth), *Hypolagus* sp. (rabbit), *Spermophilus* sp. (ground squirrel), *Paenemarmota barbouri* Hibbard and Schultz (giant ground squirrel), *Geomys* sp. (pocket gophers), *Procastoroides sweeti* Barbour and Schultz (giant beaver), *Castor* sp. (beaver), *Peromyscus* sp. (white-footed mouse), *Neotoma* sp. (wood rat), *Pliopotamys meadensis* Hibbard (Extinct muskrat), *Pliophenacomys* sp. (extinct vole), *Pliozapus*? sp. (jumping mouse), *Canis lepophagus* Johnston (extinct coyote), *Borophagus diversideus* (Cope) (extinct canid), *Satherium piscinaria middleswarti* Barbour and Schultz (extinct otter), *Lutravus* sp. (extinct mustelid), *Ischorosmilus crusifonti* Schultz and Martin (scimitar-toothed cat), *Stegomastodon mirificus* (Leidy) (short-jawed mastodon), *Pliomastodon* sp. (ancestral American mastodon), *Equus* (*Dolichohippus*) *simplicidens* (Cope) (extinct horse), *Nannippus* sp. (extinct horse), *Platygonus* sp. (peccary), *Camelops* sp. (extinct camel), *Tanupolama* sp. (extinct camel), *Titanotylopus spatulus* (Cope) (giant camel), *Capromeryx arizonensis schultzi* Skinner (ancestral pronghorn).

The presence of the more advanced muskrat *Pliopotamys meadensis* in the Broadwater Local Fauna and of the less advanced *P. minor* in the Hagerman Local Fauna suggests that the Broadwater is the younger of the two. These faunas are near the age of, or somewhat younger than, the earliest evidence of extensive continental glaciation (Boellstorff 1976; Mercer 1978), approximately 3.5 million years ago.

The Broadwater fossils come from unconsolidated sands and

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fine-grained silts that were deposited in or adjacent to a large Pliocene river system. The goose skeleton was found in the "marly" facies, suggesting an area of local ponding. In association with it were many specimens of the extinct muskrat *Pliopotamys* Hibbard, and it probably also shared its habitat with the giant aquatic beaver *Procastoroides* Barbour and Schultz and the extinct river otter *Satherium* Gazin.

MATERIAL

In addition to the fossil (see Systematics section), the material studied consisted of relevant specimens from the neoosteological collections of the University of Kansas Museum of Natural History, Division of Birds. Available was a series of 17 male and 12 female "lesser" Snow Geese from Kansas and Missouri (*Anser caerulescens caerulescens* (Linnaeus)), migrant representatives of the population breeding on the southwestern shore of Hudson's Bay (Palmer 1976:137, 140). These provided a comparatively good picture of variability in a fairly homogeneous population of modern geese. Also available were a good series (7 males, 8 females) of Ross's Goose (*Anser rossii* Cassin), a heterogeneous assemblage of Canada Geese (*Branta canadensis* (Linnaeus)), including 8 sexed examples of several of the larger subspecies and several additional specimens of the smaller ones, 3 Brant (*B. bernicla* (Linnaeus)), and 2 White-fronted Geese (*A. albifrons* (Scopoli)). These were supplemented by a loan of selected elements of a Greylag (*A. anser* (Linnaeus)) and a Bean Goose (*A. fabalis* (Latham)) from the National Museum of Natural History, Smithsonian Institution, and measurements taken for us in that museum of 3 additional Canada Geese and 3 more White-fronted Geese.

Because of the nature and preservation of the fossil's elements, the literature proved adequate for consideration of the fossil forms that seemed relevant, primary sources being almost all at hand, as well as having been conveniently summarized by Howard (1964).

Terminology is that of Howard (1929). All measurements were taken to the nearest 0.1 mm with dial calipers.

SYSTEMATICS

Order Anseriformes

Family Anatidae—Ducks, Geese, and Swans

Genus *Anser* Brisson 1760

***Anser thompsoni* new species**

Figures 1–4

HOLOTYPE: Most of a skeleton UNSM (University of Nebraska State Museum) 1110, including skull, furcula, coracoid, humerus, carpometacarpus, tibiotarsus, and other elements. Collected in 1939 by Joseph Johnson.

LOCALITY AND HORIZON: Broadwater Quarry 4 (NE ¼, Sec. 20, T.19N., R.47W.—on the Dan Bowman ranch, 8.4 km E and 1.2 km N of Broadwater, Morrill County, Nebraska), from the Lisco Member, Broadwater Formation, late Pliocene (Blancan). A cast of this specimen is on deposit at the University of Kansas Museum of Natural History (KU 24669).

DIAGNOSIS: A moderately large goose, smaller overall than the larger subspecies of modern *Branta canadensis* but larger than any known subspecies of *Anser caerulescens* or *A. albifrons*.

Compared with all other geese examined, *Anser thompsoni* is characterized by having bill from fronto-nasal hinge to tip shorter in relation to skull length (total length/bill length 2.13; 1.87–1.97 in Recent geese seen). Posterior rami of lower jaw deeper.

Furcula relatively very small.

Humerus with impression of M. brachialis anticus more elongate and more nearly parallel with the shaft; attachment of anterior articular ligament nearly circular (oval in all other geese examined); pectoral attachment not extending as far anconad.

Carpometacarpus with the process of metacarpal I longer and narrower, with its proximal edge angling proximad (as opposed to vertically or distally); distal metacarpal symphysis relatively and absolutely longer.

Tibiotarsus with the tendinal foramen beneath the supratendinal bridge circular rather than oval, and the groove for M. peroneus profundus relatively broad, shallow, and short.

MEASUREMENTS (in mm): Skull: from posteromost point of supraoccipital to fronto-nasal hinge (articulation with beak) 63.9; beak from this point to tip 56.4 (total 120.3). Lower jaw: depth of right mandibular ramus at posterior margin of coronoid process 14.4. Coracoid (left): anterior end of brachial tuberosity to middle of furcular facet 68.4. Humerus: total length 167.0 (left); greatest width near head, at right angles to shaft 36.3 (right). Ulna (left, on slab): estimated length 166 ± 1 (the olecranon process and the condyles are somewhat eroded). Carpometacarpus (left): total length 97.8; apex of process of metacarpal I to posterior margin of internal carpal trochlea 23.7. Proximal phalanx of digit II: length 40.0. Second phalanx of digit II: length 27.2. Femur (left, on slab): estimated length 83 ± 1. Tibiotarsus (left): length from external condyle to proximal articulating surface (i.e., exclusive of cnemial crests) 133.9; width across condyles 15.5; greatest anteroposterior depth between condyles 11.0. Tarsometatarsus (right, on slab): length 90.3.

ETYMOLOGY: *Anser thompsoni* is named for Max Clyde Thompson, Southwestern College, Winfield, Kansas, in grateful recognition of his many contributions to the bird collection of the University of Kansas Museum of Natural History, including its extensive osteological component.

DESCRIPTION: UNSM 1110 is a nearly complete, but moderately crushed skeleton (Fig. 1). Crushing, while not affecting most of the articular surfaces, has generally flattened the shafts of the long bones, precluding meaningful measurements of their diameters. The bones, while associated, are generally not in precise articulation. The general orientation is with the left side up. The head and neck are extended and the limbs are folded into a mass, rendering their removal and study difficult. The humeral end of the right coracoid and a fragment of the synsacrum have been displaced to the region of the head. While the sternum is missing, the undamaged furcula is nearly in correct anatomical position. The relationship of the elements is not inconsistent with the notion that the breast, viscera, and hip region were removed by some predator prior to burial.

Present in some form are all of the long bones; the shoulder girdle lacking the sternum; and the skull, lower jaw, and many of the cervical vertebrae. The synsacrum is missing, except for the above-mentioned fragment (which was removed from the slab (Fig. 1) before the photograph was taken), as are most of the ribs. The following elements, at least one of nearly every

Figure 1. The holotype, UNSM 1110, of *Anser thompsoni* new species approximately as it appeared in situ.

one successfully removed from the matrix and associated bones, are sufficiently well preserved to permit meaningful comparisons.

Skull. This is crushed and flattened in a plane between vertical and horizontal, but considerable detail is preserved, especially on the under (right) side (Fig. 2). In every respect it resembles *Anser* rather than *Branta*. The relative size is comparable to the present-day Snow Goose, but the bill is decidedly short relative to total length. Nareal opening ovoid, relatively short and broad, like *A. caerulescens* rather than *B. canadensis*. Profile of forehead and proximal bill straight as in living species of *Anser* (concave in *B. canadensis*); supraorbital region not noticeably excavated as in *Anser* (in *B. canadensis* this is moderately excavated, presumably for a nasal gland); orbit large and lachrymal short and broad as in *Anser*; lateroventral margin of maxilla moderately arched as in *A. caerulescens* and *A. albifrons* (it is nearly straight in *B. canadensis*). (The so-called "grin patch" on the bill of the Recent Snow Goose appears to be a ramphothecal feature and not an osteological one.)

Lower jaw. Rami short and massive (Fig. 2) with the posterior portion deeper than in other geese examined. Dentary curved as in *Anser caerulescens*. Coronoid process with a straight anterior margin as in *A. caerulescens* and *A. albifrons*, and a gently sloping posterior margin as in *Branta canadensis* and *A. caerulescens* (*A. albifrons* has a more abruptly curving posterior coronoid margin). Posterior margin of dentary below the lateral process of the surangular as in *Anser* (anterior to the lateral process in *Branta*).

Cervical vertebrae. These suggest a neck of average length for a species of *Anser* of comparable size. A number are missing; only 10 are visible on the slab. Recent species of *Anser* have 18, 19, or 20 (Verheyen 1955b:10–11).

Furcula. Somewhat warped and distorted, the furcular rami of *Anser thompsoni* are relatively thick, relatively short, and relatively uncurved anteroposteriorly. Somewhat surprisingly, the wishbone was clearly smaller than those of Recent *A. caerulescens*, which is considerably smaller than the fossil in other measurements; it is little larger than that of a large *A. rossii*. In short, the fossil seems to have had a remarkably small furcula, indeed, relative to Recent geese examined. Qualitatively the element seems closest to that of *A. albifrons*. (The furcula of *Branta canadensis* differs from all of those discussed

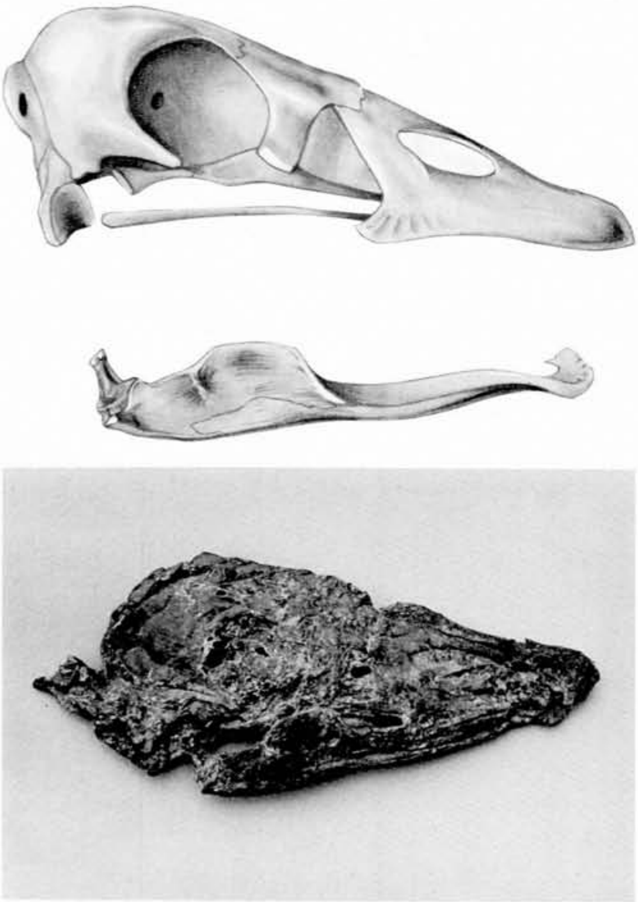

Figure 2. Upper, restoration of the skull and lower jaw of *Anser thompsoni* new species (×¾). Lower, right side of the skull of the holotype of *Anser thompsoni* new species.

in having the rami relatively long and set comparatively close together.)

Scapula. The one scapula present is robust in comparison with those of other geese examined and its pneumatic foramen is relatively very small. The posterior end is missing.

Coracoid. As do all of the living species of *Anser, A. thompsoni* has, just posterior to the brachial tuberosity, a distinct fossa that contains pneumatic foramina (Fig. 3b). However, the foramina are not as large and numerous as they are in modern species of *Anser.* In *Branta canadensis* (and its diminutive relative *B. bernicla*), the size and number of pneumatic foramina reaches an extreme; the whole furcular facet is generally undercut with pneumatic foramina along its entire posterior margin (noted by Woolfenden 1961:49). In *A. thompsoni* the furcular facet is less depressed than in *A. caerulescens.* The procoracoid is short and blunt, and the glenoid facet is narrow and *Anser*-like (less nearly circular than in *Branta*). Breakage precludes measurement of its greatest length, but the coracoid is relatively long, approximately equal to that of *B. canadensis* specimens that are considerably larger in most other dimensions.

Humerus. Humeri badly crushed but entire (Fig. 3c). They appear to have been robust. Impression of M. brachialis anticus more elongate and more nearly parallel to the shaft than in other geese examined (one specimen of Old World *Anser anser* approaches it in this respect); attachment of anterior articular ligament nearly circular (oval in other geese, so that its proximal border extends well proximad to the external condyle); ectepicondyle narrow as in *A. caerulescens*; pectoral attachment does not project as far anconad as in other geese; pneumatic foramen (proximal end) small and capital groove relatively small.

Ulna. The left ulna, exposed on the slab, possesses no relevant features other than length sufficiently intact for comparisons.

Carpometacarpus. Relatively rather long (Fig. 3a). Internal carpal trochlea does not project as far beyond the plane of metacarpal III as in Recent geese; internal ligamental fossa more nearly circular (less oval) than in other geese studied; process of metacarpal I longer and narrower than in modern geese, its proximal profile angling proximad (it angles vertically or posteriad in living geese); extensor attachment relatively large (resembling *Branta esmeralda* Burt in these particulars); distal metacarpal symphysis longer, absolutely and relatively, than in other geese examined.

Proximal phalanx, digit II. Comparatively large and broad, not as elongate, relatively, as in *Branta,* but too badly crushed to make detailed comparison useful.

Distal phalanx, digit II. This element resembles the comparable one in *Anser caerulescens.*

Femur. Still attached to slab. Imperfect and badly crushed but comparatively large and (though not precisely measurable) at least as long as that of a fairly large specimen of *Branta canadensis,* which is considerably larger in most other dimensions.

Tibiotarsus. Distal end and about two-thirds of the shaft of the left tibiotarsus present (Fig. 4a). The proximal end, badly crushed, could not be saved during removal; however, the total length was ascertained. The element is relatively very short. Also of interest is the shape of the distal articular surface when viewed end-on. In *Anser thompsoni* and *A. caerulescens* it is more compressed than in *Branta canadensis* and *A. albifrons* (the width across the condyles divided by the depth of the shaft between them in randomly selected specimens gives ratios of 0.61 in *B. canadensis,* 0.63 in *A. albifrons,* and 0.72 in both *A. caerulescens* and *A. thompsoni*). That this feature is rather variable among living geese, however, is indicated by ratios of 0.69 and 0.79 respectively for single specimens of *A. fabalis* and *A. anser.* The tendinal foramen beneath the supratendinal bridge is circular in *A. thompsoni,* rather than oval as in other geese. The external condyle is relatively rounded, and the groove for M. peroneus profundus is relatively broad, shallow, and short.

Tarsometatarsus. Relatively elongate as in *Anser caerulescens* (Fig. 4b). Detailed characters not well preserved.

DISCUSSION

COMPARISONS WITH EXTINCT TAXA

No extinct goose seems particularly close to *Anser thompsoni* on the basis of available evidence. The fossil species of greatest chronological and systematic relevance are represented by only one or a few elements (some of them referred to these species by later workers), most of which are not directly comparable.

Nearest in age is *Anser pressus* Wetmore (1933), known by a femur (length 66.9 mm) from the Hagerman Lake Beds

Figure 3. Some elements of the holotype of *Anser thompsoni* new species (×1). a, left carpometacarpus, in internal and external view. b, left coracoid, in dorsal, ventral, and internal view. c, left humerus, in palmar and anconal view.

(Blancan) of Idaho. Although the crushed condition of the present specimen prevents comparisons other than in size, *A. thompsoni* was a much larger bird (femur approximately 83 mm). It was also much larger than *Branta propinqua* Shufeldt (1892) from the late Pleistocene of Oregon (humerus 106.2 versus 167.0 mm) and *B. esmeralda* Burt (1929) from the Miocene of Nevada (carpometacarpus 77.6 versus 97.8 mm). The latter species also seems to have had a relatively shorter carpometacarpus. The shape of the process for digit II is similar in *A. thompsoni* and *B. esmeralda*. *Eremochen* Brodkorb and *Heterochen* Short (Brodkorb 1961:174; Short 1970) are distinctive extinct genera that do not appear to be closely similar to *Bran-*

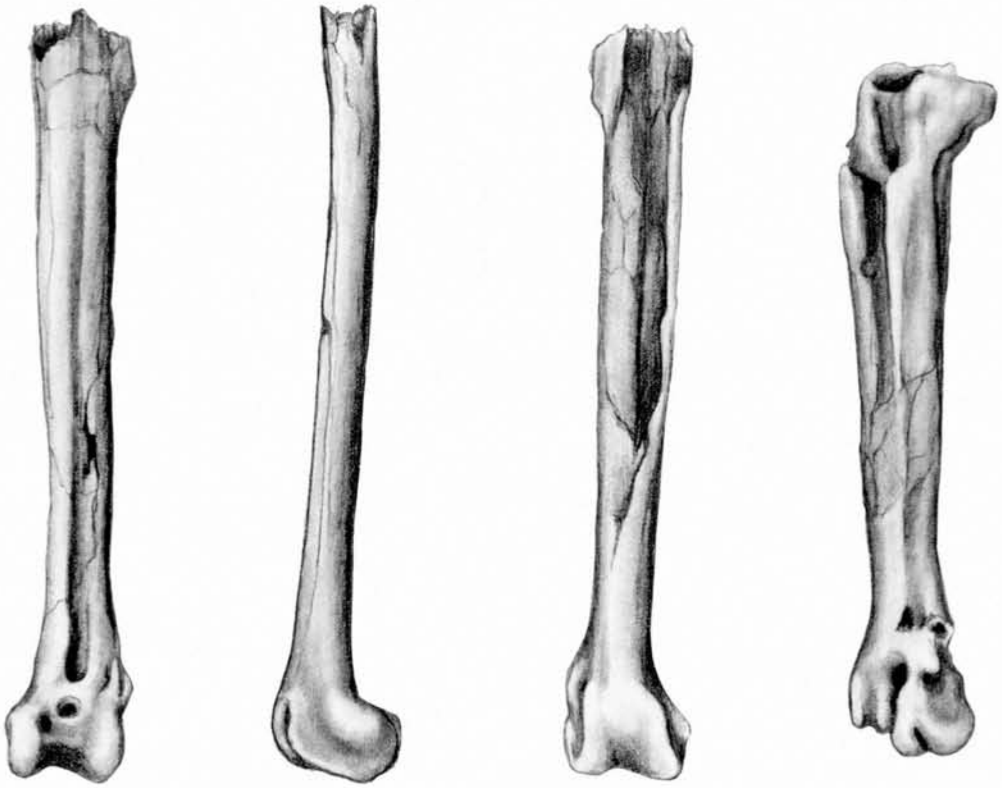

Figure 4. Some elements of the holotype of *Anser thompsoni* (×1). From left to right: anterior, internal, and posterior view of left tibiotarsus and left tarsometatarsus, posterior view.

ta or *Anser*. *Presbychen abavus* Wetmore (1930) from the Miocene of California and *B. dickeyi* L. Miller (1924) from the Pleistocene of California and Oregon are giant species much larger than *Anser thompsoni*. *Anser equitum* Bate (1916), from the late Pleistocene of Malta, if all its elements belonged to the type, was a weirdly proportioned bird perhaps incapable of flight. *Branta howardae* L. Miller (1930) from the late Miocene is based solely on the distal end of a carpometacarpus and few comparisons are possible. The distal metacarpal symphysis, however, is shorter than that of *A. thompsoni*. *Anser azerbaidzhanicus* Serebrovsky (1940), from the Pleistocene of Azerbaidzhan, USSR, apparently had a much larger cranium and more bulging frontals (see Howard 1964:269).

COMPARISONS WITH RECENT TAXA

Most if not all living geese have been recorded from the Pleistocene and one or two from earlier time (Brodkorb 1964:234–237). Recent workers are increasingly reluctant, however, to credit the existence of living species before the Pleistocene (Brodkorb 1966; Feduccia 1975). Although *Anser thompsoni* shares osteological characters with various living geese (see Systematics section), several are diagnostic, individually or in combination. Features of the carpometacarpus alone separate it from Recent forms.

Because fossil remains of birds usually consist of a few elements at most, these often fragmentary, comparisons are generally restricted to a few characters and often to relative estimates of general size. The relative completeness of *Anser thompsoni*, however, permits unusually extensive comparison, at least with Recent geese (Tables 1 and 2).

SOME STATISTICAL CONSIDERATIONS: A full-scale statistical study of proportions in modern geese, while much to be desired, is far beyond the scope of this paper. Although we restricted ourselves to readily available samples of the living geese presently numerous in continental North America, we think we have gained some insights into the probable range of dimensions in *Anser thompsoni* and its general proportions compared with some familiar living forms. A few explanations are necessary.

1. A modest, but significant, sexual difference in size required that males and females of both *A. caerulescens* and *A. rossii* be separated in statistical analysis of direct measurements (Table 1). Sexes of *Branta canadensis* and *A. albifrons* were not so separated because the sample of the former included several of the larger subspecies, while that of the latter consisted of unsexed individuals. Hence both would be expected to show exaggerated variances.

2. We combined sexes when considering relative proportions (ratios) because there was no evidence of significant sexual dimorphism in any of these species. This improved the sample sizes (Table 2).

3. Ratios, individually determined for each specimen and summed, were treated statistically in the same way as (more or less) normally distributed linear measurements. Although numerous precedents exist in similar cases (e.g., Engels 1940 and citations therein), caution is required (Simpson, Roe, and Lewontin 1960:163–165; Sokal and Rohlf 1969:17–18). In the

Table 1. Measurements (in mm) of various geese with means ± standard errors, standard deviations, and N (*Anser caerulescens, A. rossii*); or mean, N, and range (*Branta canadensis, A. albifrons*).*

Character	*Anser thompsoni* (new species)	*Anser caerulescens*	*Anser rossii*	*Branta canadensis* (large races)	*Anser albifrons*	*Anser anser*	*Anser fabalis*
Skull + bill	120.3	♂♂ 116.3 ± 0.7 2.6 (15)	♂♂ 86.2 ± 0.7 1.8 (7)	120.5 (10) 116.2–128.9	105.6 (5) 102.2–110.2	—	—
		♀♀ 111.8 ± 1.3 3.6 (8)	♀♀ 83.7 ± 1.4 3.7 (8)				
Bill	56.4	♂♂ 61.8 ± 1.3 5.2 (15)	♂♂ 44.4 ± 0.3 0.9 (7)	63.2 (7) 56.9–69.0	56.9 (2) 55.2, 58.5	—	—
		♀♀ 58.0 ± 0.4 1.0 (8)	♀♀ 42.7 ± 1.0 2.6 (8)				
Humerus	167.0	♂♂ 148.3 ± 1.2 4.9 (17)	♂♂ 128.0 ± 0.9 2.2 (6)	181.8 (11) 168.6–194.9	147.9 (5) 143.8–152.7	117.6 (1)	161.4 (1)
		♀♀ 144.0 ± 1.1 3.9 (12)	♀♀ 124.4 ± 1.5 3.9 (8)				
Ulna	166 ± 1 (estimate)	♂♂ 148.3 ± 1.2 4.9 (17)	♂♂ 127.3 ± 1.3 3.3 (7)	171.8 (11) 157.3–182.6	143.0 (5) 138.3–146.2	—	—
		♀♀ 143.5 ± 1.3 4.4 (12)	♀♀ 124.0 ± 1.7 4.1 (7)				
Carpometarcarpus	97.8	♂♂ 83.1 ± 0.9 3.5 (16)	♂♂ 73.4 ± 0.9 2.4 (7)	101.1 (10) 92.9–104.8	83.1 (5) 78.9–84.7	98.5 (1)	91.3 (1)
		♀♀ 80.0 ± 0.7 2.5 (12)	♀♀ 70.4 ± 0.7 1.9 (8)				
Femur	83 ± 1 (estimate)	♂♂ 73.0 ± 0.7 2.8 (17)	♂♂ 62.5 ± 0.5 1.2 (7)	84.1 (8) 77.8–91.9	71.1 (2) 68.4, 73.9	—	—
		♀♀ 71.1 ± 0.3 1.2 (12)	♀♀ 61.0 ± 0.8 2.1 (8)				
Tibiotarsus	133.9	♂♂ 132.5 ± 1.3 5.3 (17)	♂♂ 114.2 ± 0.9 2.3 (7)	148.6 (11) 140.7–159.8	121.7 (5) 118.7–124.2	149.6 (1)	133.4 (1)
		♀♀ 129.9 ± 1.1 3.8 (12)	♀♀ 113.2 ± 1.1 3.0 (8)				
Tarsometatarsus	90.3	♂♂ 84.0 ± 1.1 4.7 (17)	♂♂ 71.6 ± 0.5 1.2 (7)	90.9 (11) 83.6–98.8	72.4 (5) 70.6–74.5	91.9 (1)	72.9 (1)
		♀♀ 80.9 ± 0.7 2.6 (12)	♀♀ 68.8 ± 1.5 3.9 (8)				

* The abridged statistical treatment of *B. canadensis* and *A. albifrons* is explained in text.

present case, although the distributions of our ratios somewhat resemble normal ones (their coefficients of variation average somewhat smaller than those of the direct measurements), we regard their confidence limits with some suspicion and have avoided firm conjectures except where differences and *t* values were considerable.

GENERAL SIZE: Relations among the Recent taxa and their elements are observable in Table 1. Standard deviations in populations of equal variability are directly proportional to size (i.e., the mean). Thus, in comparing the fossil with Recent geese, one may infer the standard deviation (Fisher 1952) of a single specimen from that of a near relative (e.g., *Anser caerulescens,* assuming similar variability) and plot the theoretical ranges of its population within any chosen limits (here $\pm 2\sigma$ or 95 percent of a theoretically normal population). This may be done considering the single specimen either as an average, a very small, or a very large example (Simpson, Roe, and Lewontin 1960:207–208). The results, for the absolute size of the fossil humerus compared with that of the Snow Goose, are shown in Figure 5a.

Clearly, if the holotype of *Anser thompsoni* is a relatively very large example, the measurements of its population would extensively overlap those of male *A. caerulescens* and other geese of comparable size.

In short, while there is no question that *Anser thompsoni* (humerus length 167 mm) averaged very much to considerably larger than *A. caerulescens* (mean length of humerus, ♂♂, 144 mm), even given the seemingly large difference of 23 mm (16 percent above the Snow Goose mean), very extensive overlap of *individuals* is not ruled out. This assumes particular importance whenever size is the only meaningful character in a comparison, and is especially worth noting among geese, which are usually polytypic and often highly so (individual Canada Geese from various populations range from 1.3 to more than 10 kg in weight).

PROPORTIONS: Of special interest here are ratios involving the limbs and their components (Table 2), characters related to locomotion. *Anser thompsoni* lacks any conventional index of "absolute" body size (e.g., trunk length, Engels 1941:63), so we have expressed the lengths of appendicular

Table 2. Proportions of various geese (as percent) with means ± standard errors, standard deviations, and N.

Character (Ratios of lengths)	*Anser thompsoni* (new species)	*Anser caerulescens*	*Anser rossii*	*Branta canadensis* (large races)	*Anser albifrons*	*Anser anser*	*Anser fabalis*
Skull/bill	213.2	190.3 ± 2.0 8.5 (23)	196.8 ± 1.6 5.7 (11)	192.0 ± 2.2 5.8 (7)	186.9 (2) 186.5, 187.3	—	—
Ulna/humerus	99.4 (estimate)	100.0 ± 0.5 2.8 (29)	99.0 ± 0.7 2.6 (11)	94.5 ± 0.4 1.2 (11)	96.7 ± 0.7 1.6 (5)	—	—
Carpometacarpus/humerus	58.6	55.9 ± 0.2 1.0 (28)	56.7 ± 0.2 0.5 (12)	56.0 ± 0.3 0.8 (10)	56.2 ± 0.6 1.2 (5)	55.5 (1)	56.6 (1)
Femur/humerus	49.7 (estimate)	49.4 ± 0.5 2.5 (29)	48.8 ± 0.2 0.7 (12)	46.4 ± 0.4 1.2 (8)	48.2 (2)	—	—
Tibiotarsus/humerus	80.2	89.9 ± 0.4 1.9 (29)	90.0 ± 0.5 1.8 (12)	81.6 ± 0.5 1.7 (11)	82.3 ± 0.8 1.8 (5)	84.2 (1)	82.7 (1)
Tarsometatarsus/humerus	54.1	56.5 ± 0.3 1.5 (29)	55.2 ± 0.4 1.3 (12)	50.0 ± 0.5 1.7 (11)	48.9 ± 0.5 1.1 (5)	51.7 (1)	49.5 (1)
"Index of locomotion"*	140.2 (estimate)	130.7 ± 0.5 3.0 (28)	131.7 ± 0.7 2.2 (11)	140.4 ± 1.5 3.8 (7)	141.0 (2) 141.0, 141.0 145**, 146**	142**	141**
Humerus/trunk	—	77.6 (5)	80.6 (2)	76.6 (2)	79.4 (2)	—	—

* Humerus + Ulna + Carpometacarpus/Femur + Tibiotarsus + Tarsometatarsus.

** From Verheyen, 1955b.

elements as percentages of the length of the humerus. This element has been found to be a fair indicator of general body size in comparatively homogeneous groups of anseriforms (Humphrey and Clark 1964:189).

In assessing the validity of the humerus as an indicator of absolute size, we measured the trunk lengths of a few of the Recent geese in our samples and obtained humerus/trunk length ratios (Table 2). The differences found between species in these small samples are uniformly insignificant ($p < 0.20$ to 0.40). Trunk length is difficult to measure even in articulated specimens and prohibitively difficult in disarticulated ones.

For present purposes, therefore, we accept the humerus as at least a moderately good standard of overall size in these geese. Even if it were not, the ratios presented here provide direct intramembral ratios for wing elements and standardized, indirect ones for hind limb elements and intermembral comparisons. As such, all of them are directly comparable among the species considered.

Three sets of relationships are of special interest.

1. The length of the hind limb and its elements. *Anser caerulescens* and *A. rossii,* virtually sibling species, are distinctly long-legged geese. This is clearly perceptible in the field when the birds are standing. The "index of locomotion" (i.e., wing length/leg length; see Verheyen 1955b:10–12) for *A. caerulescens* compared with *Branta canadensis* in the present samples shows this very clearly ($p < 0.001$). *Anser thompsoni* differs from *A. caerulescens* in this respect, being short-legged like the Canada Goose ($0.001 < p < 0.01$), a difference also revealed by comparison of the tibiotarsus/humerus ratios (Fig. 5b).

The relative length of the leg in these geese results principally from different combinations of tibiotarsal and tarsometatarsal lengths (Table 3), since their femora seem to be comparatively uniform in relative size. In long-legged *Anser caerulescens* (and *A. rossii,* which, being relatively similar in most respects is omitted from further comparisons), the tibiotarsus and tarsometatarsus are both long. In short-legged *Branta canadensis* and *A. albifrons* (and probably in *A. anser* and *A. fabalis*), both elements are short. The fossil also has a short leg, *but this results from a very short tibiotarsus offsetting*

Table 3. Differences and their significances for each comparison of the relative length of the tibiotarsus (lower left) and tarsometatarsus (upper right) among *Anser thompsoni* and several Recent geese.*

	Anser thompsoni	*Anser caerulescens*	*Branta canadensis*	*Anser albifrons*
Anser thompsoni	—	longer n.s.	shorter $0.02 < p < 0.05$	shorter $0.01 < p < 0.02$
Anser caerulescens	shorter $p < 0.001$	—	shorter $p < 0.001$	shorter $p < 0.001$
Branta canadensis	shorter n.s.	longer $p < 0.001$	—	shorter n.s.
Anser albifrons	shorter n.s.	longer $p < 0.001$	shorter n.s.	—

* Read down (e.g., the tibiotarsus of *A. thompsoni* is relatively shorter than that of *A. caerulescens,* etc.). The letters n.s. stand for not significant.

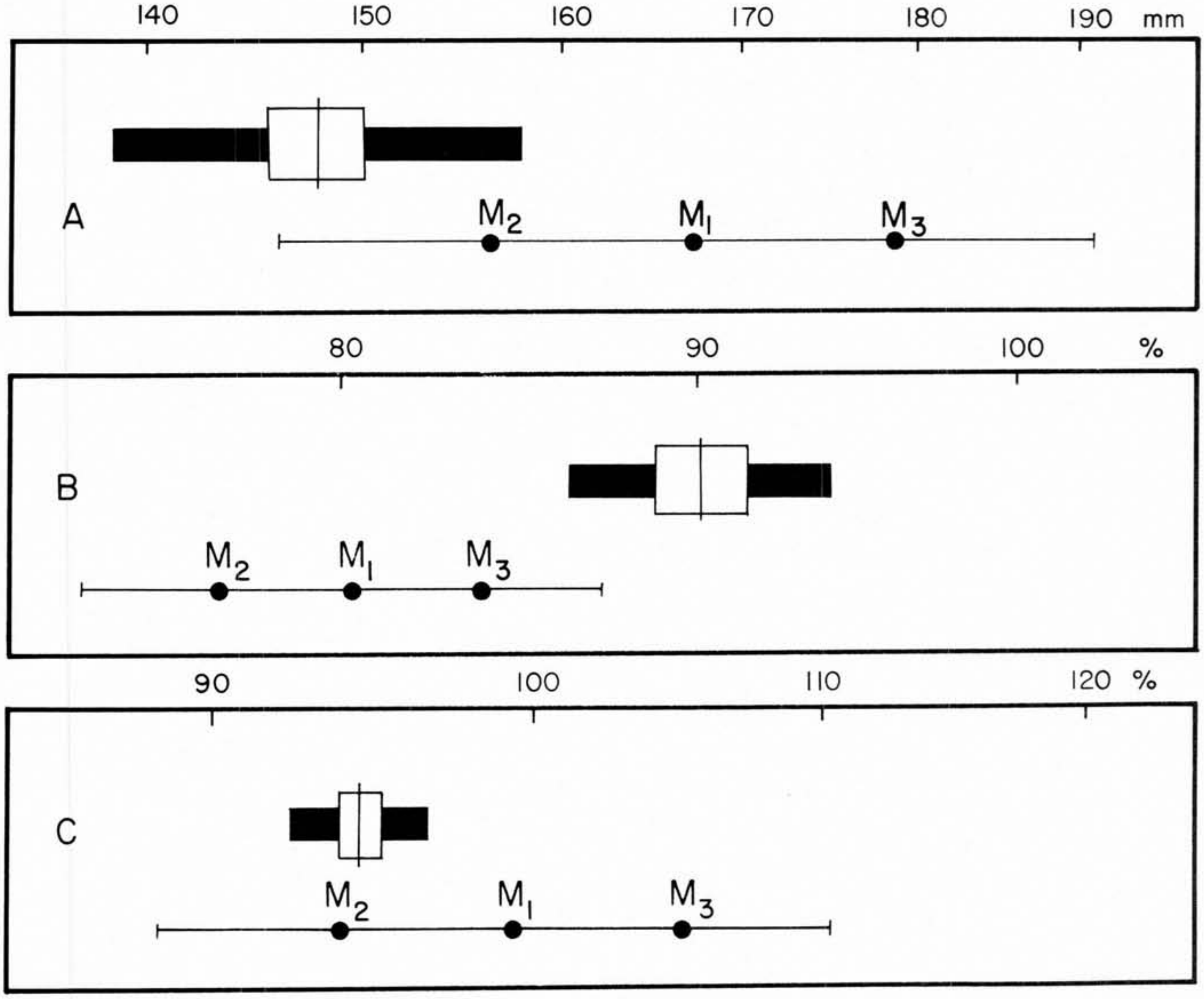

Figure 5. Some statistics of *Anser thompsoni* and Recent taxa. A, length of humerus, compared with *A. caerulescens caerulescens* males. B, length of tibiotarsus/length of humerus, compared with *A. c. caerulescens*. C, length of ulna (estimated)/length of humerus, compared with *Branta canadensis*. For Recent taxa: white boxes = mean ± 2 standard errors; black rectangles = mean ± 2 standard deviations; vertical lines = means. For *A. thompsoni* new species, M_1, M_2, and M_3 = theoretical means with the holotype regarded, respectively, as average, 2σ below, and 2σ above the mean (σ inferred from *A. caerulescens*); horizontal line = $M_1 \pm 4\sigma$. The horizontal scale is logarithmic. For details see text.

the lesser effect of a comparatively long tarsometatarsus. In Table 3 and the text, probabilities are those resulting from Student's t test of the difference between means (for its variant formula for comparing single specimens with samples, see Simpson, Roe, and Lewontin 1960:182–183; or Sokal and Rohlf 1969:224–225).

It is difficult to assess these differences in a functional context with present knowledge. Our initial tendency to regard the long legs of the Snow Goose as an adaptation for grazing per se was dampened by indications (Palmer 1976:150, 233) that the Snow Goose is more addicted than the Canada Goose (and probably more than the White-fronted Goose) to aquatic feeding. We now hazard the guess that short legs in geese are related to grazing on comparatively bare ground or in low cover on land or in shallow water, where a long neck, as in *Branta canadensis,* usefully increases the area covered. Longer legs appear better suited to marshy substrates and higher cover. *Anser thompsoni* seems to belong in the first category.

2. Relative lengths of forelimb elements. *Anser caerulescens* and *A. rossii* have long ulnae in relation to their humeri (Verheyen 1955b:10–12). In our samples this relative difference in length is highly significant when either is compared with *Branta canadensis* ($p < 0.001$). *Anser albifrons* has an intermediate ulna/humerus index, but its ulna, relatively, is still significantly shorter than that of the Snow Goose ($0.01 < p < 0.02$). With its long ulna, *A. thompsoni* resembles *A. caerulescens,* in comparison (Fig. 5c) with *B. canadensis* ($0.001 < p < 0.01$). The length of the ulna of *A. thompsoni* is approximate, but even if it were 2 mm shorter than estimated, or 164 mm, it would still be significantly longer than that of *B. canadensis* ($p < 0.02$).

The carpometacarpus of *Anser thompsoni* is also relatively

Table 1. Measurements (mm) of the coracoid of several species of *Ardea*.

Species	Length	Width of Head	Depth of Head	Width through Glenoid Facet	Width through Scapular Facet and Procoracoid	Maximum Width of Glenoid Facet
A. goliath (3)	86.3–95.5	14.7–15.3	8.3–8.8	14.9–17.3	13.3–14.1	10.7–11.3
A. howardae (type)	(80)[1]	12.8	6.4	12.3	10.3	9.4
A. sumatrana (2)	73.6–73.8	11.9–12.4	5.4–5.6	11.4–11.9	9.5–10.3	7.2–7.8
A. cinerea (9)	56.4–63.4	10.3–11.9	5.5–5.9	10.3–11.9	8.9–9.6	7.2–7.8
A. melanocephala (3)	59.7–60.5	10.5–11.2	5.2–5.9	10.5–11.0	8.2–8.7	6.0–6.9
A. pacifica (3)	47.3–48.1	10.3–10.4	4.8–5.2	9.2–9.5	8.3 (1)	6.1–6.2
A. purpurea (2)	54.7–55.4	9.0–9.2	4.1–4.6	8.7–9.8	6.9–7.7	5.4–6.7

[1] Estimate; length as preserved 40.4.

overhang; (5) glenoid facet almost flat; (6) scapular facet a deep, round cup; (7) procoracoid well developed, curved, imperforate, and unnotched; (8) triosseal canal almost flat.

Genus *Ardea* Linnaeus

As I have been unable to find generic characters in the upper part of the coracoid in the Ardeidae, the species is referred to *Ardea* Linnaeus on the basis of its very large size, which exceeds that of all known herons except the living *Ardea goliath* Cretzschmar of Africa and India (see Table 1).

***Ardea howardae* new species**

Figure 1

HOLOTYPE: Upper (cephalic) half of left coracoid, University of California Department of Anthropology, No. F504-27.

TYPE LOCALITY: Shungura, Omo Basin, southwestern Ethiopia. Shungura Formation, Member G, unit 27; age about 1.94 million years.

DIAGNOSIS: Differs from *A. goliath* as follows: (1) size about 20 percent less; (2) head less swollen but relatively wider, extending laterally almost to level of scapular facet (narrower in *A. goliath,* occupying only the medial two-thirds of the width of the bone); (3) scapular facet with lower margin horizontal, then swinging upward to glenoid facet, where it forms a prominent notch (in *A. goliath* the anterior margin of the scapular facet forms a smooth arc that continues to the glenoid facet, where it cuts only a slight notch); (4) procoracoid much less developed; (5) triosseal canal shallower.

Differs from Recent *Ardea sumatrana* Raffles of southeast Asia to Australia as follows: (1) size larger; (2) head more swollen, and relatively and absolutely wider; (3) notch separating scapular and glenoid facets much larger; (4) triosseal canal shallower.

Differs from Recent *Ardea cinerea* Linnaeus of Eurasia and Africa as follows: (1) size larger; (2) head more swollen; (3) coracohumeral groove shallower; (4) glenoid facet nearly flat (more concave in *A. cinerea*); (5) brachial tuberosity reduced, merging gradually with shaft (forms a swollen lip that overhangs posterior face of shaft in *A. cinerea*); (6) procoracoid less developed and less recurved.

Differs from Recent *Ardea melanocephala* Vigors and Children of Africa as follows: (1) size larger; (2) head of coracoid more swollen although of about the same relative width; (3) scapular facet much wider with its lateral margin curved (almost vertical in *A. melanocephala*); (4) notch separating glenoid and scapular facets much larger.

Differs from Recent *Ardea pacifica* Latham of Australia as follows: (1) size very much greater; (2) head more swollen but of similar lateral extent; (3) inner corner of head merging gradually with shaft (inner corner of head forms a swollen lip overhanging shaft in *A. pacifica*); (4) scapular facet much wider and rounder (laterally compressed in *A. pacifica,* with lateral and medial edges nearly vertical); (5) notch separating glenoid and scapular facets much more developed; (6) procoracoid less developed and slightly curved (well developed and straighter in *A. pacifica*).

Differs from Recent *Ardea purpurea* Linnaeus of southern Eurasia and Africa as follows: (1) size very much greater; (2) head more swollen with its inner corner gradually merging with shaft; (3) notch between glenoid and scapular facets larger; (4) procoracoid less developed and less recurved.

Ardea howardae is very much larger than the known Pliocene herons. These are *Ardea polkensis* Brodkorb (1955) and *Nycticorax fidens* Brodkorb (1963) from the early Pliocene of Florida, *Nyctanassa kobdoenus* Kurochkin (1976) from the early Pliocene of Mongolia, and *Botaurus hibbardi* Moseley and Feduccia (1975) from the late Pliocene of Kansas.

Ardea rupeliensis Van Beneden (1873) from the Oligocene of Belgium barely escapes being a nomen nudum and has been relegated to the Aves Incertae Sedis (Brodkorb 1978).

ETYMOLOGY: On the occasion of the 52nd anniversary of her association with the Natural History Museum of Los Angeles County, I dedicate this species to my friend Dr. Hildegarde Howard, in recognition of her many contributions to our knowledge of the fossil birds of the Pliocene/Pleistocene.

COMMENTS ON SOME OTHER FOSSILS ASSIGNED TO THE ARDEIDAE

My conclusions on the proper systematic position of some other fossils described in the family Ardeidae are presented below.

Goliathia andrewsi Lambrecht

Lambrecht (1930:30, Fig. 7) described *Goliathia andrewsi* as a new genus and species of heron based on a very large ulna from an unknown locality in the Upper Eocene/Lower Oligocene Faiyûm series of Egypt. Earlier in the same paper he erected a new genus and species of large stork, *Palaeoephip-*

Figure 1. *Ardea howardae* new species. From left to right, anterior, lateral, posterior, medial, and below, cranial views of coracoid. Length as preserved, 40.04 mm.

piorhynchus dietrichi, based on a skull and mandible from "Kasr el Querun" (=Kafr el Qeren?) in the Faiyûm. He correctly thought the ulna too small to go with the skull of the stork. He further stated that the olecranon, internal cotyla, and cubital tubercles were all weakly developed as in herons, rather than prominent as in Ciconiidae. Andrews (1907) had previously remarked that the ulna was somewhat smaller and notably stouter than that of the Recent *Ardea goliath,* but the muscle scars were similar.

It is not possible to judge the depth of the internal cotyla from Lambrecht's drawing, but it clearly shows the reduction of the olecranon and cubital tubercles. These characters are not found in species of the family Ciconiidae, but they are shared by and are even more pronounced in the Recent *Balaeniceps rex* Gould (Ardeae: Balaenicipitidae) than they are in Ardeidae.

The stoutness of the bone mentioned by Andrews is apparent in the drawing, and this too more closely resembles that of *Balaeniceps* than it does the slender ulna of Ardeidae. In respect to the muscle scars I see no trenchant differences between *Balaeniceps* and Ardeidae.

In view of the above considerations I believe that *Goliathia andrewsi* should be placed in the family Balaenicipitidae. The only previous fossil record for the family is the tentative referral of the distal end of a tibiotarsus from the Miocene of Tunisia (Rich 1974).

Ardea lignitum Giebel

This species was based on the distal half of a left femur from the Brown Coal of Rippersroda in Thuringia, Germany (Giebel 1860:152, Pl. 1, Fig. 2, erroneously called Fig. 3 in his text). He attributed the site to the Pliocene, but the formation is now placed in the Sarmatian, i.e., Upper Miocene (Thenius 1959).

Lambrecht (1933) was unable to locate any of Giebel's types so we must rely on published sources. Giebel wrote of the type (in my translation), "This so strikingly resembles the femur of the Gray Heron, *Ardea cinerea,* that comparison with other genera seems completely superfluous. Still it is not identical." He then described several differences and illustrated anterior and posterior aspects of the type.

Table 2. Measurements (mm) of the femur of several species of *Ardea* and large owls.

Species	Length	Least Width of Shaft	Distal Width
Ardea goliath (2♂♀)	126.8–135.0	10.2–10.4	23.1–23.9
A. herodias (17♂♀)	100.0–114.2	6.7–7.9	17.1–18.8
A. cinerea (9♂♀)	79.1–92.8	6.4–7.1	14.4–16.0
A. purpurea (2♂♀)	84.3–93.4	5.5–6.1	12.5–14.0
"*Ardea*" *lignitum* (1)[1]	(100)	8	18
Bubo bubo (1♀)	100.2	9.6	21.2
B. bubo (19)[2]	99.9	9.0	20.7
B. b. davidi (2–5)[3]	106.0	9.5	22.6
B. binagadensis (1)[4]	98.8	9.2	—
B. lacteus (1♀)	88.8	8.6	20.1
B. virginianus (11♂♀)	78.9–85.5	7.1–8.4	16.2–18.0
B. africanus (9♂♀)	65.0–69.6	5.3–6.0	12.4–13.8
Nyctea scandiaca (4♂♀)	82.6–90.9	7.6–8.6	16.8–20.1
N. s. gallica (2–3)[5]	92.4	8.5	19.3
Strix nebulosa (2♂♂)	83.9–84.4	5.7–6.1	15.5–15.9
S. uralensis (3)[6]	—	6.3	14.9
S. brea (4)[7]	75.6–76.6	—	—
S. varia (13♂♀)	69.6–77.2	5.6–6.2	13.1–14.7
S. intermedia (1)[8]	—	5.0	12.5
S. aluco (1♂)	59.3	4.1	10.6
S. aluco (7)[9]	—	4.6	11.2

[1] Holotype, Miocene, Germany, length estimated (Giebel 1847).

[2] Mean of Recent specimens (Mourer-Chauviré 1975:165).

[3] Mean of paratypes, Mindel stage, France (Mourer-Chauviré 1975:165).

[4] Holotype, Upper Pleistocene, Azerbaijan (Burchak-Abramovich 1965:453).

[5] Mean of paratypes, Mindel stage France (Mourer-Chauviré 1975: 162).

[6] Mean of 3 Recent specimens (Mourer-Chauviré 1975:172).

[7] Paratypes, Upper Pleistocene, California (Howard 1933:68).

[8] Referred specimen, Mindel stage, France (Mourer-Chauviré 1975:172); the holotype is a coracoid, Middle Pleistocene, Czechoslovakia (Jánossy 1972:53).

[9] Mean of Recent specimens (Mourer-Chauviré 1975:172).

For some unexplained reason the femora and some other bones of herons and owls are rather similar. Pertinent differences in the distal half of the femora of owls (both Strigidae and Tytonidae) are enumerated below.

In anterior view, (1) the external side of the external condyle of owls flares strongly laterad from the edge of the shaft (more so in *Bubo* and *Nyctea* than in *Strix* and *Tyto*), whereas in *Ardea* the condyle is more compressed and lies more nearly in line with the shaft; (2) in owls the distal notch of the external condyle is quite hidden, but it is visible in *Ardea*; (3) the lateral edge of the shaft is concave above the condyle (most so in *Bubo*), contrasting with a marked prominence in the same area in *Ardea*; (4) the intercondylar sulcus is deep and wide (especially in *Bubo* and *Nyctea*), narrow and shallow in *Ardea*; (5) the distal end of the intermuscular line shows some individual variation, but in owls it usually terminates far above the internal condyle (especially in *Bubo*), whereas in *Ardea* it continues to the proximal rim of the internal condyle.

In posterior view of the femora of owls (6) the internal condyle is relatively narrow, especially in *Bubo* (wide and long in *Ardea*); (7) the shelf of the external condyle swings gradually toward the shaft in both strigid and tytonid owls, but in *Ardea* the shelf bulges laterad before swinging to the shaft; (8) the two intermuscular lines show some individual variation in owls, but they usually merge about half way up the shaft; they remain separate in *Ardea*.

In medial and lateral views, (9) the femur is more strongly curved in owls than in *Ardea*.

Giebel's plate clearly shows characters 1–8 enumerated above, and the ninth is mentioned in his text. They were used by him to differentiate his fossil from the living *Ardea cinerea* Linnaeus, but they really prove he had an owl. In both quantitative (see Table 2) and qualitative characters the Brown Coal species is closest to the living Eagle Owl, *Bubo bubo* (Linnaeus). It must be removed from Ardeidae and placed in Strigidae as *Bubo lignitum* (Giebel), new combination.

Giebel (1847) also described eight supposedly extinct birds from the late Pleistocene in the then widely held belief that all remains from the "Diluvium" represented species that failed to survive the Noachian Flood. All appear to be synonyms of living species.

Ardea brunhuberi Ammon

This species was based on the proximal half of a left carpometacarpus from the Upper Miocene Brown Coal Formation in the clay works of Mayer and Reinhard between Deckbetten and Prüfening in Württemburg, Germany. The detailed description and photograph (Ammon 1911:33, Fig. 5) are repeated in a later and more accessible paper (Ammon 1918:30, Fig. 4).

Although the author compared it with the Recent Purple Heron, *Ardea purpurea* Linnaeus, a glance at the illustration suffices to show that this is a cormorant, not a heron. The alular metacarpal (metacarpal I) is thrust proximad, with its tip obliquely truncate as in *Phalacrocorax*, in contrast with the condition in *Ardea*, in which it is thrust less proximad and has a pointed tip. The facet for the alular digit (digit I) is very

Table 3. Measurements (mm) of the carpometacarpus of three species of *Phalacrocorax*.

Measurement	*P. brunhuberi*	*P. carbo* (n = 2)	*P. miocaenus*
Length	75 (estimate)	73.8–74.3	43.2
Height through alular metacarpal	15	14.6–14.9	9.6
Length of inner rim of trochlea	10	10.4–11.5	—
Height of alular metacarpal	5	4.0–5.0	—
Width of proximal articulation	7	6.9–7.2	5.0
Length of pisiform process	3	3.3–3.5	—

Table 4. Measurements (mm) of the coracoid of four species of *Phalacrocorax*.

Measurement	*P. praecarbo*	*P. carbo* (2)	*P. miocaenus*	*P. littoralis*
Length	75–80 (estimate)	75.0–78.3	52	54
Length of furcular facet	9	11.0–11.5	—	—
Width of furcular facet	6	7.6–8.1	—	—
Width of glenoid facet	10	10.4–10.8	—	—
Width below glenoid facet	—	10.7–11.4	6.7	8.2
Head to tip of procoracoid	20	21.1–22.5	—	—

large and deeply excavated, but in *Ardea* it is small and only slightly excavated. Furthermore, the trochlea is large (small in *Ardea*), and the external rim extends much farther proximad than in *Ardea*. It is therefore necessary to refer to this species as *Phalacrocorax brunhuberi* (Ammon), new emendation.

In his later paper Ammon (1918:28, Fig. 3) erected *Phalacrocorax praecarbo,* based on the upper half of a left coracoid from the same locality. Tables 3 and 4 show that the types of both names under discussion agree in size with the corresponding elements of European specimens of Recent *Phalacrocorax carbo* (Linnaeus). As it is unproven and highly unlikely that two species of cormorants of the same size class occurred at this site, I place *Phalacrocorax praecarbo* in synonymy with *Phalacrocorax brunhuberi*.

Phalacrocorax intermedius (Milne-Edwards 1867) from the Orléanais Sand, known only from an incomplete humerus, is slightly smaller than *P. carbo*. It is also somewhat older than *P. brunhuberi,* so I hesitate to synonymize the latter with Milne-Edward's species.

Ardeacites molassicus Haushalter

This species was based on a right humerus from the railroad cut through Miocene/Pliocene sands, between Augsburg and Landau in the former district of Algäu, southwestern Bavaria (Haushalter 1855:11, Pl. 2, Fig. 1). The type was formerly in the Munich Museum, but according to Lambrecht (1933) it has been lost. Haushalter compared it with the living European Bittern, *Botaurus stellaris* (Linnaeus), but his description is practically useless. The type is shown in palmar view, with most of the deltoid crest and the condyles badly damaged. The published measurements are length 140 mm, mid-width 7 mm. My measurements from the plate are length 140, mid-width of shaft 8, and least width of shaft 7 mm.

If the drawing is accurate, this is not a heron. The head of the humerus is too long and pointed. The deltoid crest is too long, the bicipital crest much too narrow, and the distal end is too narrow. It obviously represents a water bird of some sort, but I am unable to get it in an order, much less a family. Therefore I assign it to the Aves Incertae Sedis.

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THE AUSTRALIAN DROMORNITHIDAE: A GROUP OF EXTINCT LARGE RATITES

By Pat Vickers Rich[1]

ABSTRACT: The Dromornithidae was a family of large ground birds, presumably ratite, that has a Miocene to Pleistocene (minimum age, 26,000 years B.P.) record in Australia. Five genera are now known, including *Dromornis, Genyornis, Ilbandornis, Bullockornis,* and *Barawertornis*. The known forms range in size and agility from slightly larger than, and about as gracile as, the living emu, to truly gigantic, ponderous forms such as *Dromornis stirtoni* that rivaled or exceeded the size and proportions of the Malagassy elephant bird (*Aepyornis maximus*). Dromornithids and emus (Casuariidae) appear in the record simultaneously in the Miocene, the former ranging over most of Australia and reaching their greatest known diversity in the Miocene. Detailed osteological analyses of this group indicate that it is monophyletic, and more closely related to the Casuariidae, including emus, than to any other avian family.

The family Dromornithidae has been known for some time in Australia (Mitchell 1839), but because specimens were few and poorly preserved, little attention was given this group until recently. This paper presents a brief history of work on the dromornithids, familial and generic diagnoses, and hypotheses for phylogenetic relationships within the Dromornithidae as well as between the dromornithids and other avian families.

The first known reference to dromornithids lies in the oral traditions and art of the Aborigines. Tindale (1951) and Hall et al. (1951) noted traditions among the Tjapwurong tribe in western Victoria concerning "mihirung paringmal," or giant emus that supposedly lived "long ago when the volcanic hills [of the Western District of Victoria] were in a state of eruption." Some lava flows in this area are as young as 8000 years B.P. (Gill 1972). Temporal overlap of the dromornithids with Aborigines at about 26,000 years B.P. has recently been confirmed (Lancefield Swamp, Victoria; Gillespie et al. 1978), and younger records would not be surprising.

The first convincing evidence of a group of ratite birds distinct from the Casuariidae in Australia was the spectacular discovery in 1892 of partial skeletons in Pleistocene sediments of Lake Callabonna, South Australia. Newton (1893) reported this find, and subsequently Stirling (1896) and Stirling and Zietz (1896, 1900, 1905) described the Callabonna material as a new genus and species, *Genyornis newtoni*. Prior to this work all evidence of the extinct dromornithids, including the namesake of the family from Peak Downs in Queensland, *Dromornis australis* (Owen 1872, 1874), consisted of isolated and often fragmentary specimens. All of the specimens came from localities restricted to the eastern half of Australia.

Information on the Dromornithidae remained sparse until the middle of the twentieth century. Several expeditions into central and northern Australia in the mid-1950's and thereafter led to the discovery of three new genera: *Barawertornis, Ilbandornis* and *Bullockornis* (Rich 1979). Additional specimens of the previously known genera *Dromornis* and *Genyornis* were also recorded.

The dromornithids can now be delimited on the basis of the osteological material presently available, and meaningful comparisons with other ratite groups can be detailed. The trackways of probable dromornithids from southeastern Australia (Rich and Green 1974; Rich and Gill 1976) and a possible dromornithid egg from Pleistocene dune deposits in Western Australia offer negligible diagnostic data, however.

Abbreviations used are: AM, Australian Museum, Sydney; CPC, Commonwealth Palaeontological Collections, Bureau of Mineral Resources, Canberra; SIAM, American Museum of Natural History, Department of Vertebrate Paleontology Field Number, New York; UCMP, University of California, Museum of Paleontology, Berkeley.

DIAGNOSTIC FEATURES OF THE DROMORNITHIDAE

The dromornithids comprise a group of medium-sized to truly gigantic ground birds that were endemic to Australia from at least the Miocene until the late Pleistocene, perhaps as late as the Holocene. The smallest form, *Barawertornis tedfordi,* was about the size of the living ostrich or slightly smaller. The largest, *Dromornis stirtoni,* equaled or possibly exceeded the weight of any bird previously known (Fig. 1), including *Aepyornis maximus,* but was surpassed in height by the moas of New Zealand. Limb proportions vary from the massive-limbed *Dromornis stirtoni,* to the moderately slender, elongate-limbed *Genyornis,* to the extremely gracile-limbed *Ilbandornis lawsoni*. *Barawertornis* is restricted to the early

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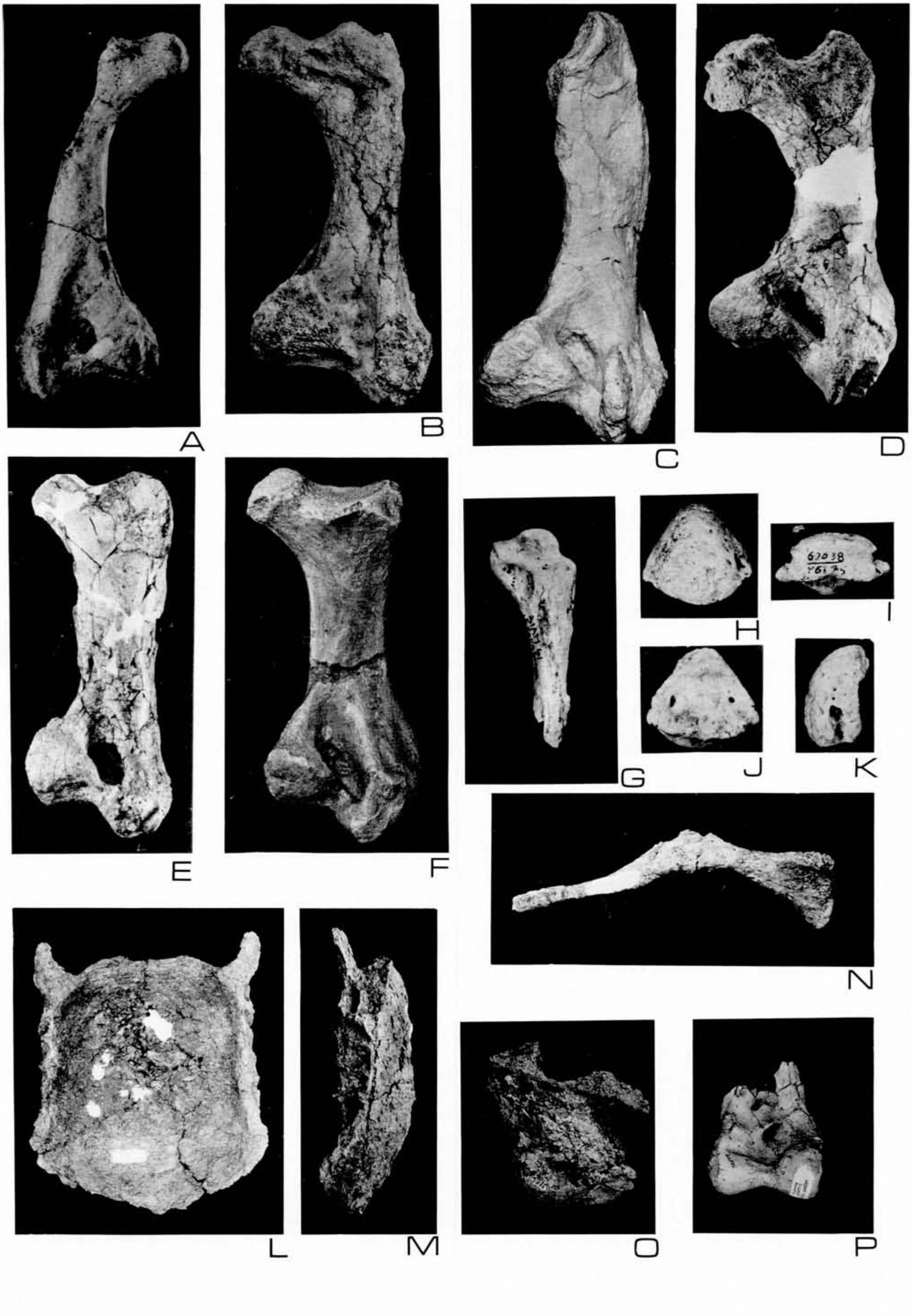
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Miocene, *Bullockornis* to the late Miocene, *Ilbandornis* to the late Miocene or early Pliocene, *Dromornis* to the late Miocene and Pliocene, while *Genyornis* is restricted to the Pleistocene. The stratigraphic distribution of the dromornithids is summarized in Figure 2, and Figure 3 shows their geographic distribution.

The dromornithids were ratites in the *classic* sense, in that they lacked a true keel on the sternum. No palatal region of the skull is known, however, and allocation of this group to the palaeognathous birds is based entirely upon the similarities of their postcranial skeletons to those of emus and cassowaries. Vertebrae are also relatively rare elements, and in no specimen is a complete vertebral series known. The dromornithids can be characterized from their known elements by the following combination of characters: (1) sternum more elongate than broad with costal area occupying 60 percent of the lateral margin; (2) sternal notches lacking; (3) articulation of sternum with scapulocoracoid restricted to far lateral margins of anterior border of sternum; (4) glenoid facet of scapulocoracoid and entire wing greatly reduced, decidedly more than in ostriches and rheas; (5) humerus lacking well defined articular surfaces; (6) radius and ulna fused at several points along their shafts; (7) carpometacarpus lacking intermetacarpal space and with only one phalangeal articulation; (8) synsacrum of moderate width, not broad as in moas and aepyornithids; (9) synsacrum with articulation of hindlimb about midway between anterior and posterior ends, in contrast to condition in struthionids, where this articulation lies forward of midpoint, and in apterygids, where it lies posterior to midpoint; (10) pubes, ischia, and ilia subequal in posterior extension; (11) pubes not fused as in struthionids; (12) pubes fuse with ischium and in turn with ilium in adult specimens to produce elongate ilioischiatic fenestra and short ischiopubic fenestra, a condition found elsewhere within the ratites only in aepyornithids; (13) femur with trochanter projecting about same distance proximad of shaft as head; (14) femur with external condyle moderately exceeding internal condyle in distal extension, but not as disproportionately as in rheas and ostriches; (15) femur lacking massive muscle scars in popliteal area, thus differing from the femora of moas and aepyornithids; (16) femur with internal condyle with distalmost extension occurring anterior to condylar midpoint, approaching elliptical shape with major axis forming acute angle with posterior margin of shaft (semicircular in shape in emus, moas, elephant birds; distally flattened in rheas, ostriches); (17) femur with condyles of equal depth; (18) tibiotarsus not decidedly mediolaterally compressed near proximal end; (19) tibiotarsus with inner cnemial crest extending far proximad to proximal articular surface; (20) tibiotarsus with supratendinal bridge present, differing from those of all other ratites except moas, and tendinal canal centrally located; (21) tarsometatarsus with hypotarsal region broad and triangular in shape in proximal view, with two shallow hypotarsal canals located near medial and lateral boundaries of hypotarsus (this arrangement differs from the rectangular structure dissected by a single, deep canal found in moas and kiwis, the laterally offset hypotarsus of ostriches and rheas, and the low, rectangular hypotarsus of aepyornithids); (22) tarsometatarsus with single, prominent ridge extending most of length of posterior surface (this differs markedly from the short, double ridges in moas and kiwis, the short, narrow ridge in rheas and ostriches, and the absence of a ridge in aepyornithids); (23) tarsometatarsus without articulation for metatarsal I, indicating the absence of the first digit; (24) tarsometatarsus with three trochleae present, although internal trochlea often quite reduced; (25) pes with phalangeal count of 3-4-4, not the more characteristic ratite count of 3-4-5, and a tendency in at least the geologically younger forms (*Ilbandornis* and *Genyornis*) to develop blunted, hooflike unguals, rather than claws with a triangular or rounded cross section.

RELATIONSHIPS OF THE DROMORNITHIDAE TO OTHER AVIAN FAMILIES

In a recent paper (Rich 1979) I used three different methods of analysis in an attempt to determine the relationship of the Dromornithidae to the remaining ratites. Although I distinctly favor Method I, other methods that have frequently been used in phylogenetic analysis were explored to determine if all methods resulted in similar conclusions. In the first method a phenetic analysis based on the postcranial skeleton was performed initially to determine the family most closely related to the ratites, and their probable nearest relatives, the tinamous (*Tinamidae*) (Bock 1963). Then—using the definition that primitiveness was defined by common occurrence of a character in both the ratites and their nearest sibling group, the tinamous—an analysis to determine whether a character was primitive or derived was performed (see Rich 1979 for the data input for all analyses, and detailed tables summarizing the results).

The second method involved surveying all of the ratites and defining as primitive the most commonly occurring state for each character. Those characters that occurred rarely within the ratites were considered derived or advanced. Theoretically, this method would help to determine phyletic branching, where a derived character or suite of characters is held by three or less families. Derived characters that appeared early

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Figure 1. A selection of diagnostic bones of Dromornithidae from mid- to late Cenozoic deposits of Australia. Femora of: (a) *Barawertornis tedfordi*, CPC 7341 (Type), Riversleigh, Queensland, Miocene (distal width 87 mm); (B–C) *Bullockornis planei*, CPC 13844 (Type) and CPC 13845 respectively, Bullock Creek, Northern Territory, Miocene (distal widths 160 mm and >152 mm); (D) *Dromornis stirtoni*, CPC 13851 (Type), Alcoota, Northern Territory, Late Miocene or early Pliocene (distal width 202 mm); (E) *Ilbandornis woodburnei*, CPC 13850 (Type) Alcoota, Northern Territory, late Miocene or early Pliocene (distal width 112 mm); (F) *Dromornis australis*, AM F10950, Peak Downs, Queensland, probably Pliocene (distal width 120 mm); (G) *Genyornis newtoni*, SIAM 61, proximal right humerus, Lake Callabonna, South Australia, Pleistocene (depth from external to internal tuberosity 25 mm); (H–K) *Ilbandornis* sp., UCMP 67038, characteristic ungual phalanx of pes, Alcoota, Northern Territory, late Miocene or early Pliocene (total length 28 mm); (L–M) *Dromornis stirtoni*, UCMP 113049, sternum, Alcoota, Northern Territory, late Miocene or early Pliocene (maximum width across sternocoracoidal processes approx. 225 mm); (N) *Dromornis stirtoni*, UCMP 113050, scapulocoracoid, Alcoota, Northern Territory, late Miocene or early Pliocene (total length >239 mm); (O) *Ilbandornis lawsoni*, UCMP 70118, proximal view of left tibiotarsus, Alcoota, Northern Territory, late Miocene or early Pliocene (maximum depth about 88 mm); and (P) *Ilbandornis* sp., UCMP 70649, distal end, right tibiotarsus, Alcoota, Northern Territory, late Miocene or early Pliocene (distal width 76 mm).

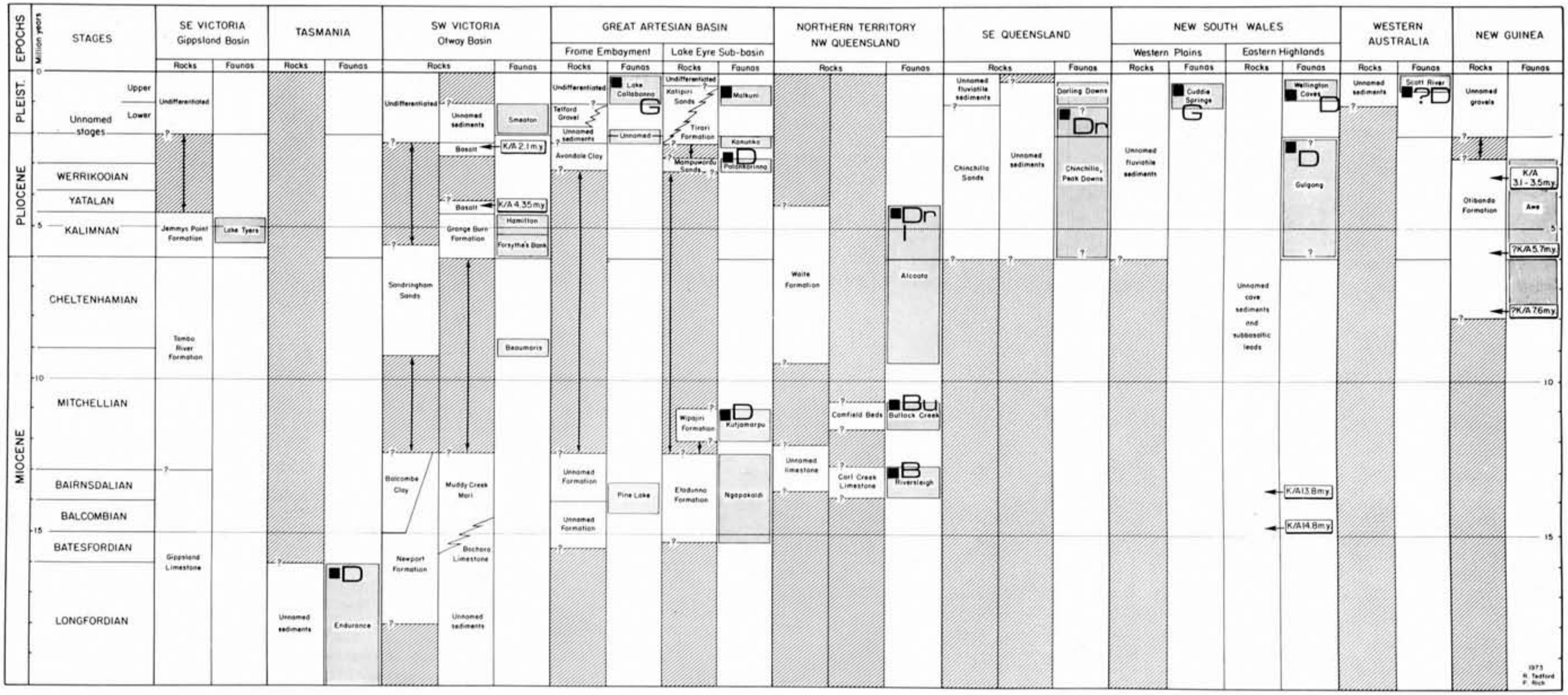

Figure 2. Stratigraphic distribution of the Dromornithidae in Australian Cenozoic deposits. Black squares represent occurrences of most dromornithid material. B, *Barawertornis*; Bu, *Bullockornis*; Dr, *Dromornis*; D, *Dromornithidae*; G, *Genyornis*; I, *Ilbandornis*. Modified from Rich (1979).

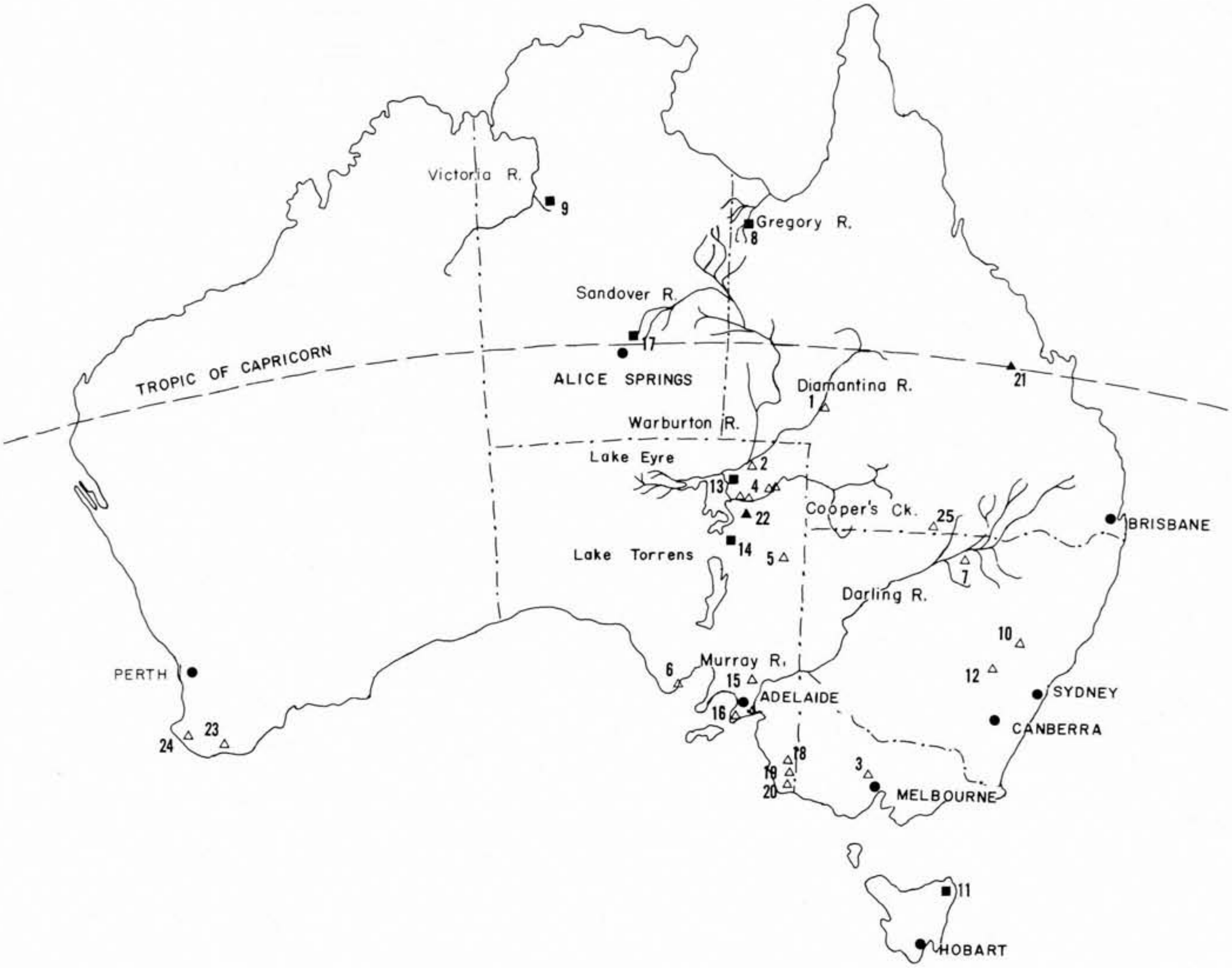

Figure 3. Geographic distribution of the Dromornithidae in Australia. △, Pleistocene; ▲, Pliocene; ■, Miocene localities. Same abbreviations for generic names as in Fig. 2. (1) Diamantina River, D; (2) Warburton River, D; (3) Lancefield, D; (4) Cooper Creek, D; (5) Lake Callabonna, G; (6) Brother's Island, Pt. Lincoln, G; (7) Cuddie Springs, G; (8) Riversleigh, B; (9) Bullock Creek, Bu; (10) Canadian Lead (Gulgong, Mudgee), D; (11) Endurance Pit, South Mt. Cameron, D; (12) Wellington Caves, D; (13) Lake Ngapakaldi, D; (14) Snake Dam Locality, D; (15) Baldina Creek, G; (16) Normanville (Salt Creek), G; (17) Alcoota, Dr and I; (18) Big Cave (Naracoorte), D; (19) Penola, D; (20) Mt. Gambier, D; (21) Peake Downs, Dr; (22) Lake Palankarinna, D; (23) Scott River, ? D; (24) Mammoth Cave, D; (25) Thornbindah, D.

in the history of ratites, however, and thus possibly were possessed by a large number of the members of this group, would be misinterpreted by this method.

The third method involved an initial phenetic analysis of 56 characters (chosen because they could be used to diagnose the Dromornithidae; Rich 1979). The 56 characters studied were summed for each ratite group regardless of their polarity (primitive or advanced (=derived)), in essence a strictly numerical taxonomic approach. Only the sternum, synsacrum, and hindlimb elements were considered because of the lack of information about other elements of various fossil groups, and because of the near or total loss of the forelimb in the Dinornithidae-Emeidae lineage as well as its marked reduction in other ratites.

The primary purpose of using the three different methods was the determination of the avian group most closely related to the Dromornithidae. Thus, relationships between the remaining ratite groups are only briefly mentioned in the following discussion.

The analysis using Method I indicates that the Dromornithidae share decidedly more derived characters (19 of the 56 studied) with the Casuariidae (including emus) than with any other ratite family, but that the two families share few primitive characters (7) (see Table 1). The Casuariidae and the Dromornithidae show a large number of derived characters within the ratites, with 33 and 38 (respectively) of the 56 characters derived rather than primitive. The Struthionidae and Rheidae have nearly the same number of derived characters (37 and 33, respectively), but the Aepyornithidae, Apterygidae, Dinornithidae-Emeidae have fewer derived characters (30, 23, and 22, respectively). Among the 19 derived characters shared between the Casuariidae and Dromornithidae are four unique to these two groups. These are: (1) synsacrum with ilium, ischium, and pubis all protruding about the same dis-

Table 1. Number of characters of the sternum, synsacrum, and hindlimb shared by the ratites and their sibling group, the Tinamidae. Method I approach.

a. Shared derived characters (determined by lack of occurrence in the Tinamidae).

	Struthionidae	Rheidae	Casuariidae	Dromornithidae	Aepyornithidae	Apterygidae	Dinornithidae-Emeidae
Struthionidae	—	—	—	—	—	—	—
Rheidae	26	—	—	—	—	—	—
Casuariidae	16	18	—	—	—	—	—
Dromornithidae	8	11	19	—	—	—	—
Aepyornithidae	13	11	13	12	—	—	—
Apterygidae	9	12	13	9	10	—	—
Dinornithidae-Emeidae	10	10	9	10	11	9	—

b. Shared primitive characters (determined by common occurrence in both ratites and Tinamidae).

	Struthionidae	Rheidae	Casuariidae	Dromornithidae	Aepyornithidae	Apterygidae	Dinornithidae-Emeidae
Struthionidae	—	—	—	—	—	—	
Rheidae	13	—	—	—	—	—	
Casuariidae	8	15	—	—	—	—	
Dromornithidae	4	8	7	—	—	—	
Aepyornithidae	7	10	13	7	—	—	
Apterygidae	9	18	20	9	17	—	
Dinornithidae-Emeidae	12	17	19	13	20	29	

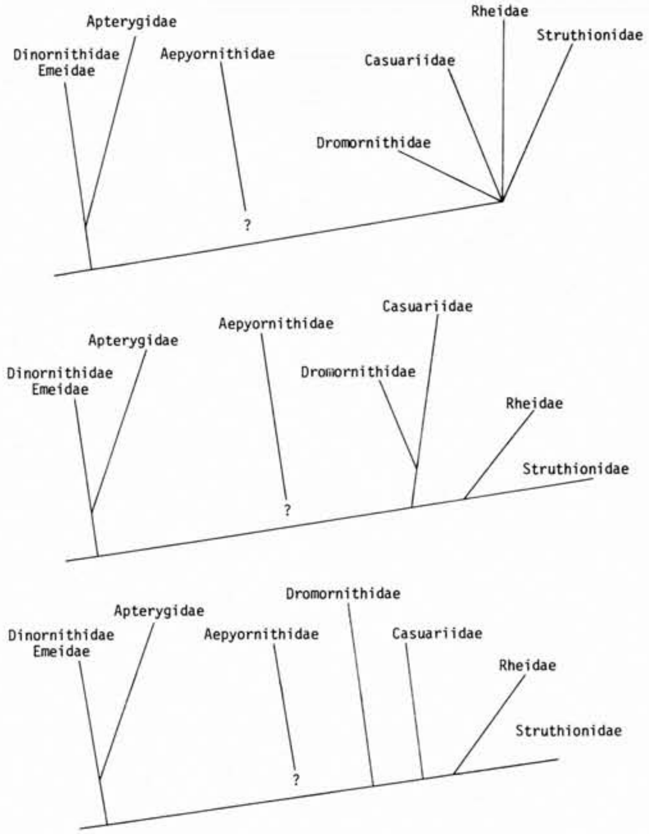

Figure 4. Phylogenetic hypotheses expressing possible interrelationships of the ratites.

tance posteriad; (2) femur with internal condyle triangular, or elliptical closely approaching triangularity, with apex forming distalmost projection of condyle; (3) tibiotarsus with inner cnemial crest extending far proximad of proximal articular surface; and (4) tarsometatarsus with hypotarsus and intercotylar prominence extending about equal distances proximad to proximal articular surfaces. The remaining 15 derived characters shared between Casuariidae and Dromornithidae are likewise shared with at least one and often more ratite groups.

For each group of ratites, the following number of the 56 characters mentioned above for Method III were present in the derived condition using the Method I approach: Struthionidae 37; Rheidae 33; Casuariidae 33; Dromornithidae 38; Aepyornithidae 30; Apterygidae 23; Dinornithidae-Emeidae 22.

Thus, the analysis of Method I indicates that the Dromornithidae are most closely related to the Casuariidae. A single, common ancestral stock could have given rise to each of these two groups, and two separate colonizations within Australia-New Guinea are not necessary to account for their presence. The Australian ratites appear decidedly distinct from the New Zealand moas and kiwis (which form a close-knit osteological group) and are apparently the most primitive of all the ratite groups. The Casuariidae, but not the Dromornithidae, in turn share a large number of derived characters with the Struthionidae (16 and 8, respectively) and Rheidae (18 and 11, respectively), which are quite closely related to one another (sharing 26 derived characters). Without further, more expanded analysis, however, it is difficult to determine how many of the characters shared by the Struthionidae-Rheidae and the Casuariidae are the result of convergent evolution. Three phyletic hypotheses are suggested (Fig. 4) based on the Method I approach.

The Method II approach, i.e., using commonality of a char-

Table 2. Number of derived characters (determined by commonality of occurrence within the ratites) of the sternum, synsacrum, and hindlimb shared by several ratite groups. Method II approach.

	Struthionidae	Rheidae	Casuariidae	Dromornithidae	Aepyornithidae	Apterygidae	Dinornithidae-Emeidae
Struthionidae	—	—	—	—	—	—	—
Rheidae	9	—	—	—	—	—	—
Casuariidae	2	2	—	—	—	—	—
Dromornithidae	1	2	7	—	—	—	—
Aepyornithidae	4	1	3	6	—	—	—
Apterygidae	1	0	2	1	1	—	—
Dinornithidae-Emeidae	3	2	1	7	4	8	—

Table 3. Number of unweighted characters of the 56 studied by Rich (1979) that are shared by the various ratite groups. Method III approach.

	Struthionidae	Rheidae	Casuariidae	Dromornithidae	Aepyornithidae	Apterygidae	Dinornithidae-Emeidae
Struthionidae	—	—	—	—	—	—	—
Rheidae	39	—	—	—	—	—	—
Casuariidae	24	33	—	—	—	—	—
Dromornithidae	12	19	26	—	—	—	—
Aepyornithidae	20	21	26	19	—	—	—
Apterygidae	18	30	33	18	27	—	—
Dinornithidae-Emeidae	22	27	28	23	31	38	—

acter within the ratites to indicate primitiveness and rarity to indicate a derived or advanced condition, reinforced many of the conclusions reached in the Method I analysis, although not all were in agreement. The Dromornithidae shared the greatest number of derived characters (7) with both the Casuariidae and the Dinornithidae-Emeidae, but only one with the Apterygidae (see Table 2). The suggested similarity between moas and dromornithids can perhaps be accounted for by size and functional similarities, a result of convergent evolution. Using Method II, casuariids clearly share far more characters considered to be derived with dromornithids than with any other ratite group, and the relationship between the moas and kiwis of New Zealand is strongly supported.

Method III, the numerical taxonomic approach, also reinforced several of the relationships suggested by the two previous methods, but obscured or contradicted others (Table 3). The Dromornithidae still shared more characters (26) with the Casuariidae, but the Casuariidae shared more characters with the Rheidae (33) and the Apterygidae (33) than with any other ratite group. Method III suggests that the Struthionidae and Rheidae are more similar to one another than to any other ratite group (sharing 39 characters), as are the moas and kiwis (sharing 38 characters). The Aepyornithidae share the most characters with the Dinornithidae.

GENERIC RELATIONSHIPS WITHIN THE DROMORNITHIDAE

As illustrated above, three different types of phylogenetic analysis suggest that the Dromornithidae share the greatest number of similarities with the Casuariidae (Fig. 4). Because of this, I also evaluated the characters of the latter group when I considered intra-dromornithid relationships.

In my analyses, a character was considered to be primitive within the family Dromornithidae if it was shared by both the dromornithids and the casuariids, or in some cases if it frequently occurred in a wide range of avian families. Additionally, a second criterion used in some analyses was to assume a character to be primitive within the dromornithids if it was the more common state in this group. All of these methods of determining the polarity of a character, i.e., whether primitive or advanced, have been discussed in numerous publications (Kluge and Farris 1969; Kluge 1971; Schaeffer et al. 1972; Hecht 1976). Time was *not* a factor that influenced determination of whether a character was primitive or advanced. In fact, one of the oldest occurring dromornithids, *Bullockornis*, appears to be one of the most specialized in the family. Once the primitive or advanced nature of each character or character complex was estimated, a phylogeny was derived based upon the minimum number of alterations to a primitive morphotype needed to produce the five genera and eight species known for the family. Analysis was restricted to the femur and tarsometatarsus because these are the only elements represented for all of the dromornithid genera, and most species. In Figure 5, 21 characters of these two elements are tabulated for each of the dromornithid genera as well as *Dromaius*, a casuariid genus. The phylogeny implied in Figures 5 and 6 resulted from analyses using the following two approaches.

First, an analysis of the dromornithid complex using commonality of occurrence within the Dromornithidae as an indicator of primitiveness was performed. The results are summarized in the following paragraphs (see Figs. 7 and 8 for illustrations of the femur, tibiotarsus, and tarsometatarsus).

Barawertornis, the oldest known dromornithid from Miocene sediments in the Northern Territory, is the most primitive and the smallest known member of the family, having 14 of the 21 characters summarized in Figure 5 in the primitive state. This genus is presumably specialized over the postulated primitive morphotype for the Dromornithidae in that on the femur, the internal condyle is broader than the external (char. 22),[1] the fibular condyle protrudes only moderately laterad (char. 15), the popliteal area is deep (char. 14); and, on the tarsometatarsus, trochleae II and IV are subequal in distal extension (char. 9).

The remaining dromornithids, including *Dromornis, Ilbandornis, Genyornis,* and *Bullockornis,* are derived with respect to *Barawertornis* because on the femur, the neck is not decidedly constricted (char. 3), the internal condyle has a decidedly elliptical shape (char. 18); and on the tarsometatarsus, trochlea II is moderately to highly reduced (char. 11).

Within the above lineage it is evident that *Dromornis, Ilbandornis,* and *Genyornis* are closely related and form a natural grouping separate from *Bullockornis*. Shared derived characters for this former lineage include the femur with the medial surface of the internal condyle decidedly ridged (char. 19), and the fibular condyle extending as far or nearly as far posteriad as the internal condyle (char. 26); and the tarsometatarsus with trochlea III moderately to decidedly broader than trochlea IV (char. 16).

Although decidedly more derived than *Barawertornis*, the *Dromornis-Ilbandornis-Genyornis* lineage, even if its most specialized member (*Genyornis*) is considered, does not possess as many derived characters within the Dromornithidae as does *Bullockornis* (12 out of 21, *Genyornis*; 14 out of 21, *Bullockornis*).

Bullockornis, with two species, is characterized by having the following derived characters: femur with shaft deep (char. 10), long axis of the external condyle nearly in line with the

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[1] Character numbers refer to those cited by Rich (1979) in a detailed analysis of the Dromornithidae. Of the 200 characters analyzed, only a few were actually useful in the final phylogenetic analyses.

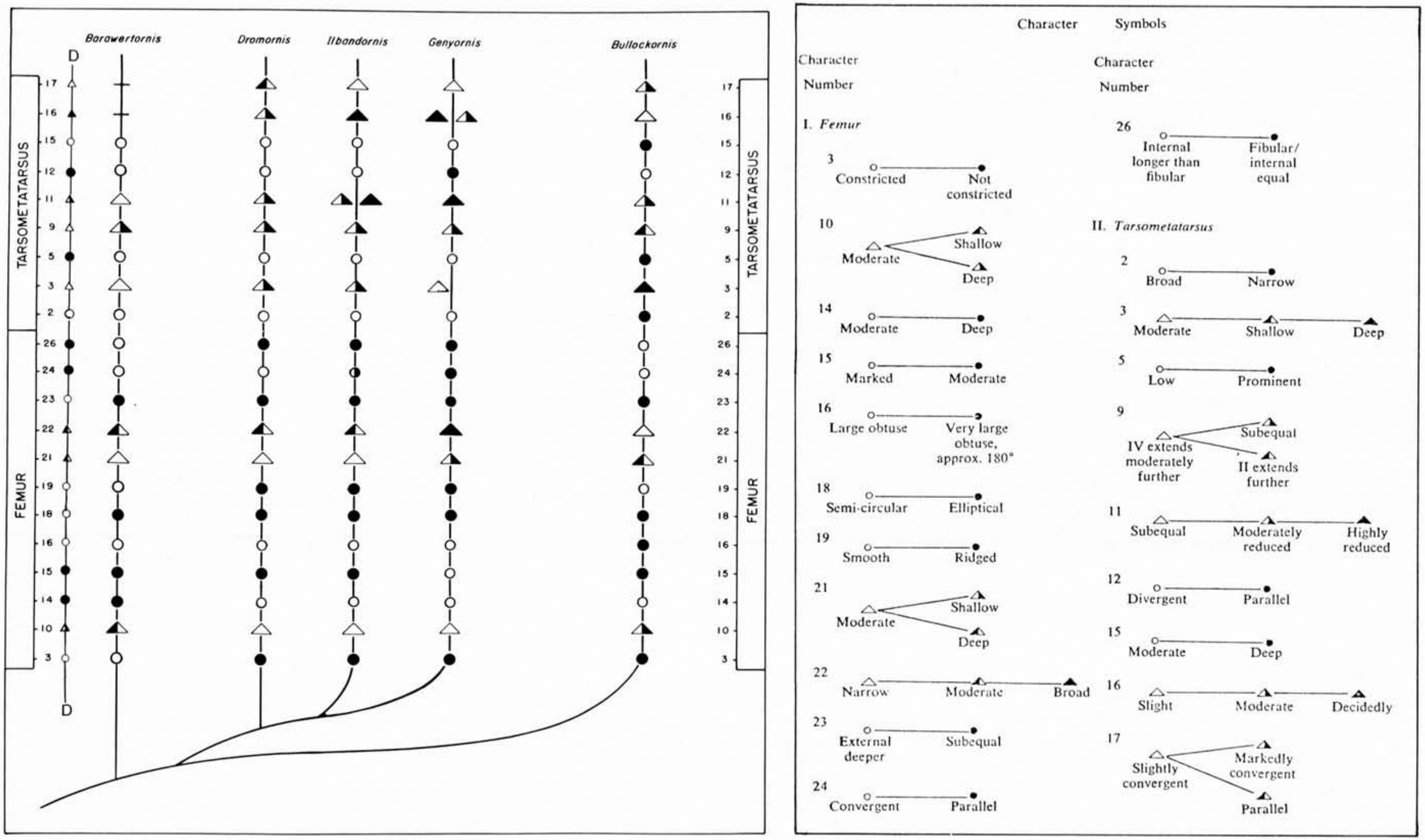

Figure 5. Distribution of characters used in constructing phylogenetic hypotheses for the Dromornithidae, based on the hindlimb. Character numbers refer to those used by Rich (1979); only a few of those analyzed were useful for phylogenetic interpretation. D, *Dromaius* (Casuariidae). Femur characters evaluated include: (3) degree of narrowing at neck, (10) degree of anteroposterior compression of shaft, (14) depth of popliteal area, (15) degree of lateral protrusion of fibular condyle, (16) angle formed between proximodistal axis of external condyle and long axis of shaft, (18) shape of internal condyle, (19) nature of distal one-fourth of internal shaft surface and internal condyle, (21) degree of anteroposterior compression of condyles with respect to width of distal end, (22) width of external condyle with respect to internal, (23) comparative depths of internal and external condyles, (24) degree of anterior convergence of long axes of condyles, (26) comparative posterior extension of fibular and internal condyles. Tarsometatarsus characters evaluated include: (2) width of intertrochlear space between trochleae III and IV, (3) depth of shaft, (5) prominence of subhypotarsal ridge, (9) comparative extension distad of trochleae II and IV, (11) reduction of trochlea II with respect to III and IV, (12) relative orientation of medial and lateral margins of trochlea II, (15) depth of trochlea III, (16) width of trochlea III with respect to width of trochlea IV at their anteroposterior midpoints, (17) degree of posterior convergence of lateral and medial margins of trochlea III.

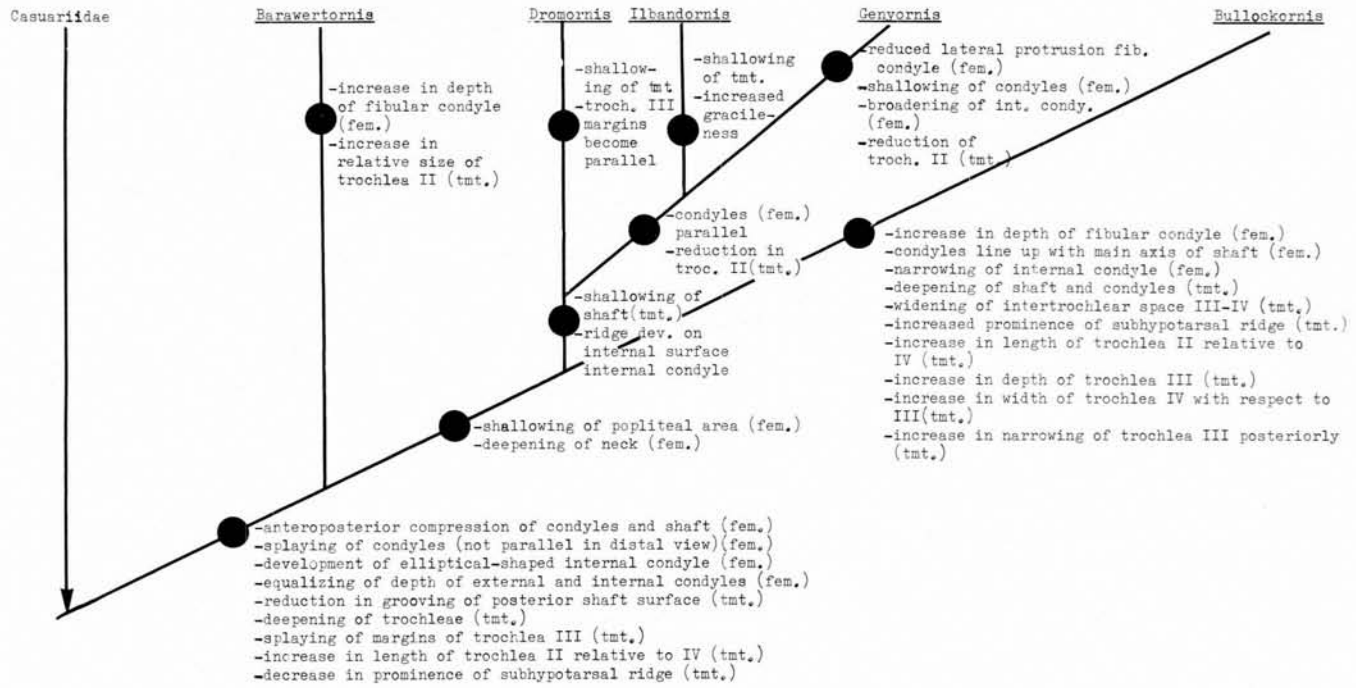

Figure 6. Phylogenetic hypothesis expressing possible interrelationships of the genera of dromornithids. Major changes occurring from most primitive (*Barawertornis*) to most advanced genera are enumerated.

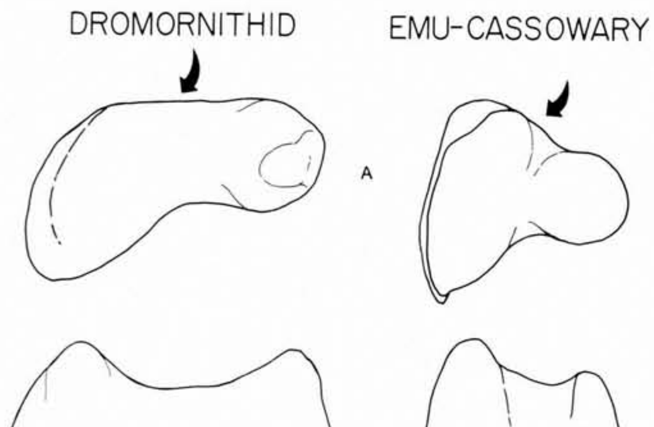

Figure 7. Comparison of femora of Dromornithidae and Casuariidae. A, proximal view; B, distal view; C, medial views.

long axis of the shaft (char. 16), and the internal and external condyles nearly subequal in depth (char. 23); tarsometatarsus with intertrochlear space between trochleae III and IV broad (char. 2), the subhypotarsal ridge prominent (char. 5), trochlea III extremely deep (char. 15), and the medial and lateral margins of trochlea III markedly convergent posteriorly (char. 17).

The second analytical approach used the common occurrence of a character state within the nearest sibling group, the Casuariidae, to indicate the primitive state of a character and produced the results described below.

Barawertornis has the greatest number of characters in a primitive state (11), even though two could not be evaluated, and *Bullockornis* the least (5). This reinforces the interpretation of the previous analysis. The following trends for the dromornithids are suggested by this analysis. In the femur there is a broadening of the neck region, and overall anteroposterior compression of shaft and distal end (*Bullockornis* may well be primitive in having a deep shaft, contrary to the suggestion of the previous analysis, or the deep condition is secondarily derived), a shallowing of popliteal area, an increase in lateral protrusion of external condyle, a decrease in twisting of condyles away from long axis of shaft, the development of an elliptical internal condyle (viewed medially), a broadening and narrowing of the internal condyle relative to width of external condyle, an increase in depth of external condyle so it becomes subequal in depth to internal condyle, and, in distal view, the long axes of condyles become parallel.

In the tarsometatarsus there is a decrease in the relative separation of trochleae III and IV, a deepening of shaft, a decrease in prominence of subhypotarsal ridge, an increase in distal extension of trochlea II, a reduction in size of trochlea II and thus in size of second digit, an increase in depth of trochlea III, and an increase in width of trochlea IV with

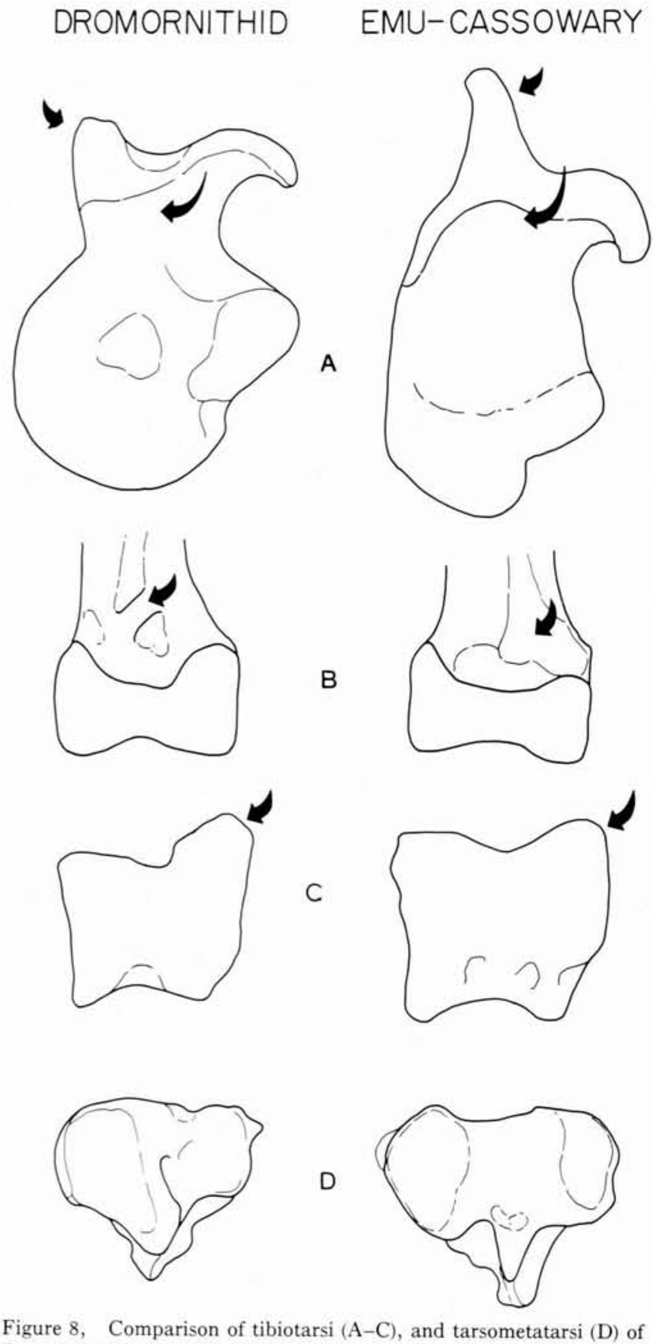

Figure 8, Comparison of tibiotarsi (A–C), and tarsometatarsi (D) of Dromornithidae and Casuariidae. A, D, proximal views; B, anterior views; C, distal views.

respect to trochlea III, and thus an equalization in the size of the two digits.

Other trends that occur at some time within the dromornithid lineage (but just when and in which genera is difficult to determine because of the lack of complete enough specimens of some genera) after it diverged from the cassowary and emu lineage include: (1) deepening and strengthening of the lower jaw, (2) deepening of the atlas vertebra, (3) flattening of the sternum and reduction in area of scapulocoracoid contact, as well as slight overall reduction in size of scapulocoracoid (the scapula and coracoid become more in line with one another), (4) equalization of overall dimensions of radius and ulna, and lengthening of both relative to humerus, (5) decrease in depth of synsacrum dorsal to acetabulum and an increase in depth of pubic bar, (6) increase in mediolateral compression of cnemial crests and a decrease in depth of internal cnemial crest of tibiotarsus, (7) development of a supratendinal bridge on tibiotarsus (or retention from ancestral stock that gave rise to both Casuariidae and Dromornithidae), (8) increase in depth of internal condyle on tibiotarsus, and (9) development of hooflike ungual phalanges on digits and loss of one phalanx in digit IV, resulting in a phalangeal formula for the pes of 3-4-4.

SUMMARY

The family Dromornithidae is composed of five genera and eight species of extinct ground birds restricted to the middle and late Cenozoic of Australia (Figs. 2 and 3). Although some forms were only slightly larger than their closest relatives, the emus and cassowaries, one form may have exceeded the weight of the largest known bird, *Aepyornis maximus* of Madagascar.

The history of the dromornithids extends back only into the Miocene, but the presence of four genera in the Miocene indicates that the group had its origins much earlier. The fossil record for most Cenozoic vertebrates in Australia is poorly known before the Miocene because of a lack of known older localities, a result of the geology of the Australian continent and the inaccessibility of certain areas that have paleontological promise.

The use of three different methods of phylogenetic analysis consistently suggested that the Dromornithidae were most closely related to the only other Australian ratite group, the Casuariidae. The dromornithids are quite distinct from the moas (Dinornithidae-Emeidae) of New Zealand and probably originated from a common stock with the Casuariidae, and possibly the Rheidae and Struthionidae. The ancestral form may have been advanced over that which gave rise to the moas, kiwis, and elephant birds. It is conceivable that a single ancestral stock on the Australian landmass could have given rise to both the casuariids and dromornithids, and two invasions are not an absolute requirement to account for the Australian ratite diversity. If such an event took place during the early to mid-Cretaceous, the ancestral form could conceivably have flown or walked between Australia and the remaining southern continents when tenuous connections still existed between these land masses.

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THE PRESENT STATE OF KNOWLEDGE OF THE CENOZOIC BIRDS OF ARGENTINA[1]

By Eduardo P. Tonni[2]

ABSTRACT: An annotated list by age and a summary by order of the Cenozoic birds of Argentina is presented. A re-evaluation of fossil taxa over which there has not been general agreement as to systematic position allows the following conclusions: (1) *Neculus rothi* Ameghino 1905 is a synonym of *Palaeospheniscus gracilis* Ameghino 1899; (2) *Palaeoapterodytes ictus* Ameghino 1905 is a synonym of *Palaeospheniscus bergi* Moreno and Mercerat 1891; (3) *Eudromia* and perhaps *Nothura* are present in Montehermosan sediments of Buenos Aires Province; (4) *Phalacrocorax pampeanus* Moreno and Mercerat 1891, from late Pleistocene deposits of Buenos Aires Province, is assignable to the living species *P. brasilianus*; (5) *Dryornis pampeanus* Moreno and Mercerat 1891 is a vulturid closely related to *Vultur*.

Preliminary analysis of new material currently under study reveals (1) an anseriform that shows affinities with the Tachyerini from late Oligocene–early Miocene marine deposits of Patagonia; (2) that the earliest known specimens of phorusrhacoids appear in Casamayoran (early Eocene) deposits of Patagonia.

RESUMEN: Se presenta una lista anotada por edad y un resumen por orden de las aves cenozoicas de Argentina. La reevaluación de los taxa fósiles sobre los cuales no hay un consenso respecto a su posición taxonomica permite llegar a las siguientes conclusiones: (1) *Neculus rothi* Ameghino 1905 es sinónimo de *Palaeospheniscus gracilis* Ameghino 1899; (2) *Palaeoapterodytes ictus* Ameghino 1905 es sinónimo de *Palaeospheniscus bergi* Moreno and Mercerat 1891; (3) *Eudromia* y quizás *Nothura* están presentes en sedimentos Montehermosenses de la Provincia de Buenos Aires; (4) *Phalacrocorax pampeanus* Moreno and Mercerat 1891, de dépositos del Pleistoceno tardío de la Provincia de Buenos Aires es asignado a la especie viviente *P. brasilianus*; (5) *Dryornis pampeanus* Moreno and Mercerat 1891 es un vultúrido de cercana relación a *Vultur*.

Un análisis preliminar de material nuevo actualmente en estudio revela (1) un anseriforme con afinidad a los Tachyerini de depósitos marinos de Oligoceno superior–Mioceno inferior de Patagonia; y (2) que los primeros especímenes conocidos de phorusrhacoides aparecen en los depósitos casamayorenses (Eoceno tardío) de Patagonia.

The record of Cenozoic birds of Argentina is the most complete for any region of South America. Most of the described forms come from Patagonia, in southern Argentina, thus limiting the record geographically. This has resulted in a restricted knowledge of the origin and evolution of certain groups, especially those presently endemic to the Neotropical Region. In addition, the record for the rest of South America is limited primarily to the Pleistocene (for a brief review of fossil birds of South America see Campbell 1979).

At the end of the 1800's and the beginning of the 1900's Florentino Ameghino described most of the known taxa of Cenozoic Argentinian birds, but his work requires revision as a result of new contributions. A partial revision has been accomplished for his extensive work on the fossil mammals of Argentina, but this is not the case with the birds. Only two avian groups, the phorusrhacoids and penguins, have been extensively revised. Any revisions have been hindered in part by the scattering of the original materials in different Argentinian and foreign institutions, a fact that has brought about great confusion.

It must be re-emphasized here, as I have before (Tonni 1973), that there are no uniform taxonomic criteria to be used with both fossil and Recent birds. In general, the criteria of paleontologists differ from those of neontologists. When one considers some of the taxonomic problems regarding Recent birds, e.g., polytypic species, sibling species, sexual dimorphism, etc., it is evident that the study of fossil birds, the remains of which are generally very fragmentary, can be difficult and complicated. This points again to the need to revise the works of the pioneer authors using the more rigorous taxonomic standards of today.

In spite of these difficulties, and others common to the study of all fossil vertebrates, the paleontological record of Argentinian birds contributes valuable data on some groups, especially if the information is taken as a whole and not partially.

A list of Cenozoic Argentinian birds, with their geographic

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and stratigraphic data, follows. The scheme of Land Mammal Ages follows that of Pascual et al. (1965) and Pascual and Odreman Rivas (1973); see Figure 1. The Tertiary stratigraphic chart has recently changed significantly, but it is not the purpose of the present study to discuss these changes and the reader is referred to the pertinent literature (Berggren and Van Couvering 1974; Marshall et al. 1977; Marshall et al. 1979). I have re-studied most of the material of doubtful taxonomic position. Preliminary data on material under study are included.

Those orders with a fossil record sufficient to warrant additional comments are discussed at the end of this paper. Such a discussion based on the data presently available is quite limited, and will remain so until the study of fossil birds from the Neotropical Region becomes the focus of attention of a greater number of investigators.

SYSTEMATIC LIST OF CENOZOIC BIRDS FROM ARGENTINA

CASAMAYORAN

Order Phoenicopteriformes, Family Presbyornithidae:

Presbyornis antiquus (Howard 1955)

LOCALITY AND HORIZON: Cañadón Hondo, near Paso Niemann, Chubut Province. Casamayor Fm.

Presbyornis pervetus Wetmore 1926

LOCALITY AND HORIZON: Cañadón Hondo, near Paso Niemann, Chubut Province. Casamayor Fm.

REMARKS: This specimen was described as *Telmabates howardae* by Cracraft (1970). See Feduccia (1976) for further information.

Order Opisthocomiformes, Family Onychopterygidae:

Onychopteryx simpsoni Cracraft 1971

LOCALITY AND HORIZON: Cañadón Hondo, near Paso Niemann, Chubut Province. Casamayor Fm.

REMARKS: Brodkorb (1978:215) places this species in Aves Incertae Sedis.

DIVISADERAN

Order Ralliformes, Family Cunampaiidae:

Cunampaia simplex Rusconi 1946

LOCALITY AND HORIZON: 500 m west of Mina Atala, Departamento de Las Heras, Mendoza Province. Divisadero Largo Fm.

REMARKS: The systematic position of *Cunampaia simplex* is uncertain. The general concensus is to place it in its own family within the Ralliformes, but its placement within the order varies according to the author. Patterson and Kraglievich (1960:12) state that "su posición dentro de la Clase es por ahora incierta"—"its position within the Class is for now uncertain." Wetmore (1960) considered the position of the family within the Ralliformes to be uncertain, a treatment followed by Cracraft (1968). Brodkorb (1967) includes the family Cunampaiidae in the suborder Cariamae.

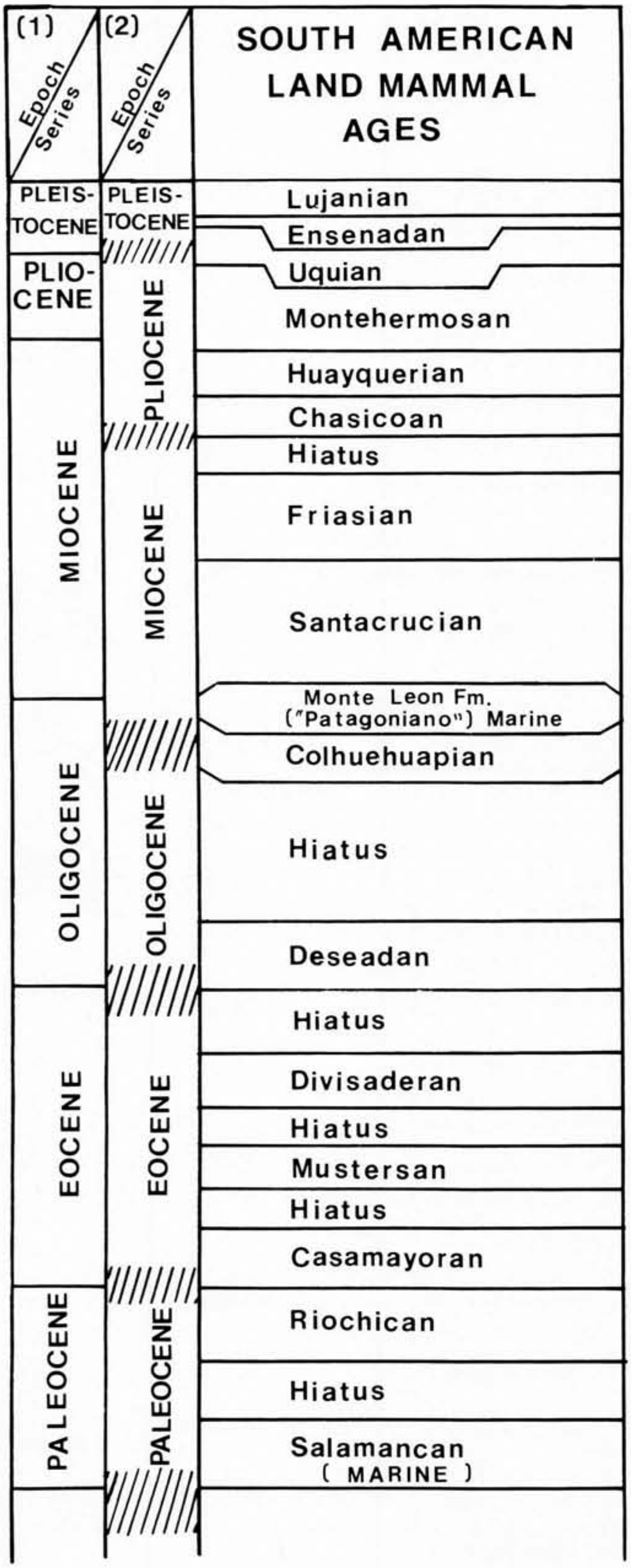

Figure 1. Cenozoic epochs and the corresponding South American Land Mammal Ages. Modified from Marshall et al. 1977. (1) After Berggren and van Couvering (1974). (2) After Savage (1975).

DESEADAN

Order Ardeiformes, Family Ciconiidae: *Ciconiopsis antarctica* Ameghino 1899

LOCALITY AND HORIZON: Santa Cruz Province. Deseado Fm. ("Guaranitic Fm." of Ameghino).

Order Pelecaniformes, Family Cladornithidae: *Cladornis pachypus* Ameghino 1895

LOCALITY AND HORIZON: Río Deseado, Santa Cruz Province. Deseado Fm.

Order Anseriformes, Family *incertae sedis*: *Teleornis impressus* Ameghino 1899

LOCALITY AND HORIZON: Santa Cruz Province. Deseado Fm.

Loxornis clivus Ameghino 1895

LOCALITY AND HORIZON: Río Deseado, Santa Cruz Province; Río Chico, west of Puerto Visser, Chubut Province. Deseado Fm.

Order Accipitriformes, Family Accipitridae?: *Cruschedula revola* Ameghino 1899

LOCALITY AND HORIZON: Golfo de San Jorge, Santa Cruz Province. Deseado Fm.

REMARKS: This species is based on the proximal end of a right scapula, as noted by Brodkorb (1964), and not on a tarsometatarsus as stated by Ameghino. The material is not very diagnostic, but its placement in the Accipitridae is probable.

Climacarthrus incompletus Ameghino 1899

LOCALITY AND HORIZON: Santa Cruz Province. Deseado Fm.

REMARKS. This species is based on the distal end of a right tarsometatarsus that lacks the external trochlea, most of the middle trochlea, and the posterior portion of the internal trochlea. This species can be tentatively assigned to the Accipitridae on the basis of characters of the internal trochlea; i.e., it extends distad more than the middle trochlea and has a marked concavity in the proximal part of the internal margin.

Order Ralliformes

The family sequence followed here corresponds to that of Cracraft (1968, 1969).

Family Aramidae: *Aminornis excavatus* Ameghino 1899

LOCALITY AND HORIZON: Río Deseado, Santa Cruz Province. Deseado Fm.

Loncornis erectus Ameghino 1899

LOCALITY AND HORIZON: Río Deseado, Santa Cruz Province. Deseado Fm.

Family Phorusrhacidae: *Andrewsornis abbotti* Patterson 1941

LOCALITY AND HORIZON: Cabeza Blanca, Chubut Province. Deseado Fm.

Family Brontornithidae: *Physornis fortis* Ameghino 1895

LOCALITY AND HORIZON: Río Deseado, Santa Cruz Province. Deseado Fm.

Family Psilopteridae: *Smiliornis penetrans* Ameghino 1899

LOCALITY AND HORIZON: Santa Cruz Province. Deseado Fm.

Pseudolarus guaraniticus Ameghino 1899

LOCALITY AND HORIZON: Santa Cruz Province. Deseado Fm.

Family Cariamidae: *Riacama caliginea* Ameghino 1899

LOCALITY AND HORIZON: Santa Cruz Province. Deseado Fm.

"PATAGONIANO"

The age of the marine sediments generally referred to as "Patagoniano" has been a matter of great controversy. According to Camacho (1974), the "Patagoniano" is divisible into the following units: the San Julián Formation, strata with *Monophoraster* and *Venericor,* and the Monte León Formation. The type locality of the San Julián Fm. is in the Gran Bajo of San Julián, Santa Cruz Province. The latter two units outcrop from the Golfo de San Jorge and Santa Cruz and Chubut Provinces, northwards to the proximity of Trelew and the lower course of the Río Chubut. These three units were referred by Camacho to the early Eocene, late middle Eocene, and late Oligocene, respectively.

Bertels (in press) considers the San Julián Formation to be late Eocene to early Oligocene in age. Cione and Exposito (in press), on the basis of their study of an icthyofauna from a unit referred to the *Monophoraster* and *Venericor* strata of the Golfo de San Jorge, state that that unit is at least late Oligocene in age.

Marshall et al. (1977), on the basis of isotopic dating of the sediments of the Santa Cruz and Colhuehuapí Formations that respectively overlie and underlie the Monte León Fm., assigns the Monte León Fm. to the late Oligocene.

Recently, Riggi (1979) recognized a single formational unit (Patagonia Fm.) in the "Patagoniano" sediments. He divides the Patagonia Fm. into two members, the San Julián and the Monte León, both of Oligocene age.

Unfortunately, the penguin remains described by Ameghino and Moreno and Mercerat lack precise geographic and stratigraphic data. There are precise data on only the material studied by Simpson (1946, 1972) from the lower course of the Río Chubut, between Gaiman and Trelew. Field work carried out by the author in this area (Tonni in press) has verified that the associated icthyofauna indicates the deposits are at least late Oligocene to early Miocene in age.

There is no conclusive evidence demonstrating that the penguins from the more southerly outcrops (Golfo de San Jorge, San Julián) are of a different age. The following nine species are all from the "Patagoniano."

Order Sphenisciformes, Family Spheniscidae:

Palaeospheniscus gracilis Ameghino 1899

LOCALITY: Golfo de San Jorge, Trelew, Gaiman; Chubut Province.

REMARKS: *Neculus rothi* Ameghino 1905 is included in this species. The holotype is strongly weathered and thus the trochleae appear to be disproportionately small. Other supposedly diagnostic characters, e.g., tarsometatarsus very flattened anteroposteriorly with the anterior surfaces of the trochleae lying in the same plane, the intertrochlear notches deep, and a large metatarsal facet, correspond to those of the holotype of *P. medianus* (=*P. gracilis*). The transverse diameter at mid-shaft of the tarsometatarsus of "*Neculus rothi*" is 12 mm, while that of the holotype of *P. medianus* (=*P. gracilis*) is 13.5 mm. Consequently, taking into consideration individual size variation, *N. rothi* lies within the size range of *P. gracilis*, of which it is a synonym.

Palaeospheniscus patagonicus Moreno and Mercerat 1891

LOCALITY: Golfo de San Jorge, Trelew, Gaiman; Chubut Province.

Palaeospheniscus wimani (Ameghino 1905)

LOCALITY: San Julián, Santa Cruz Province.

Palaeospheniscus bergi Moreno and Mercerat 1891

LOCALITY: Golfo de San Jorge, Trelew; Chubut Province.

REMARKS: *Palaeoapterodytes ictus* Ameghino 1905, which was based on the proximal portion of a strongly weathered right humerus, is included in this species. Simpson (1946) stated *P. ictus* was indeterminate, and that *Palaeoapterodytes* (=*Apterodytes*) was probably a synonym of *Palaeospheniscus* or some other genus from the same beds. Simpson questioned placing *Palaeoapterodytes* in synonymy with *Palaeospheniscus* because "[*Palaeoapterodytes*] probably did not have a bipartite tricipital fossa, which is always present in *Palaeospheniscus*" (Simpson 1972:29). A re-evaluation of the holotype verifies that the tricipital fossa is undoubtedly bipartite and that the specimen shares the size range and other morphological characteristics of the humeri referred to *Palaeospheniscus bergi*.

Chubutodyptes biloculata Simpson 1970

LOCALITY: Cerro Castillo, Chubut Province.

Paraptenodytes antarcticus (Moreno and Mercerat 1891)

LOCALITY: The mouth of the Río Santa Cruz, Santa Cruz Province.

Paraptenodytes brodkorbi Simpson 1972

LOCALITY: San Julián, Santa Cruz Province.

Paraptenodytes robustus (Ameghino 1895)

LOCALITY: La Cueva, San Julián, Santa Cruz Province; Gaiman, Chubut Province.

Arthrodytes grandis Ameghino 1901

LOCALITY: San Julián, Santa Cruz Province.

Order Procellariiformes, Family Procellariidae?:

Argyrodyptes microtarsus Ameghino 1905

LOCALITY AND HORIZON: Río Seco, Santa Cruz Province. Basal "Patagoniano."

REMARKS: This species was based upon a supposedly associated distal half of a tibiotarsus and a distal half of a femur. As pointed out by Simpson (1946, 1972), it is not from a species of the Sphenisciformes. Its placement in the Procellariidae, following Brodkorb (1963), is quite probable.

Order Anseriformes, Family Anatidae:

Anatidae new genus new species

LOCALITY: Gaiman, Chubut Province.

REMARKS: This new genus new species, with affinities with the Tachyerini, is currently being described (Tonni in press).

SANTACRUCIAN

Order Rheiformes, Family Rheidae:

Opisthodactylus patagonicus Ameghino 1895

LOCALITY AND HORIZON: Santa Cruz Province. Santa Cruz Fm.

REMARKS: Patterson and Kraglievich (1960) correctly concluded that *Opisthodactylus*, type of the family Opisthodactylidae Ameghino 1895, is not a phorusrhacoid, but a rhea. Brodkorb (1963) included the Opisthodactylidae in the Rheiformes.

Order Pelecaniformes, Family Pelecanidae:

Liptornis hesternus Ameghino 1895

LOCALITY AND HORIZON: Santa Cruz Province. Santa Cruz Fm.

Order Ardeiformes, Family Plataleidae:

Protibis cnemialis Ameghino 1891

LOCALITY AND HORIZON: Monte Observación, Santa Cruz Province. Santa Cruz Fm.

Order Anseriformes, Family Anatidae:

Eoneornis australis Ameghino 1895

LOCALITY AND HORIZON: Monte Observación, Santa Cruz Province. Santa Cruz Fm.

Eutelornis patagonicus Ameghino 1895

LOCALITY AND HORIZON: Monte Observación, Santa Cruz Province. Santa Cruz Fm.

Order Accipitriformes, Family Accipitridae:

Thegornis musculosus Ameghino 1895

LOCALITY AND HORIZON: Tagua Quemada, Santa Cruz Province. Santa Cruz Fm.

Thegornis debilis Ameghino 1895

LOCALITY AND HORIZON: Corriguen-Kaik, Santa Cruz Province. Santa Cruz Fm.

REMARKS: Brodkorb (1964) includes these two species in the subfamily Circinae. If this is correct, they represent the oldest record for the subfamily.

Family Falconidae:

Badiostes patagonicus Ameghino 1895

LOCALITY AND HORIZON: "Patagonia." Santa Cruz Fm.

Order Galliformes, Family Cracidae:

Anisolornis excavatus Ameghino 1891

LOCALITY AND HORIZON: "Southern Patagonia." Santa Cruz Fm.

Order Ralliformes, Family Phorusrhacidae:

Phorusrhacos longissimus Ameghino 1887

LOCALITY AND HORIZON: La Cueva, Tagua Quemada, Monte Observación, Río Shehuén; Santa Cruz Province. Santa Cruz Fm.

REMARKS: See Brodkorb (1967) for the synonymy of the species included in this family and all other large extinct South American ralliforms.

Family Palaeociconiidae:

Palaeociconia cristata Moreno and Mercerat 1891

LOCALITY AND HORIZON: Monte León, Tagua Quemada, Monte Observación, La Cueva; Santa Cruz Province. Santa Cruz Fm.

Family Psilopteridae:

Pseudolarus eocaenus Ameghino 1891

LOCALITY AND HORIZON: "Patagonia." Santa Cruz Fm.

Psilopterus australis Moreno and Mercerat 1891

LOCALITY AND HORIZON: Killik-Aike, Monte León, Monte Observación, Take Harvey, La Cueva, Corriguen-Kaik, Tagua Quemada, Karaiken; Santa Cruz Province. Santa Cruz Fm.

Psilopterus communis Moreno and Mercerat 1891

LOCALITY AND HORIZON: Monte Observación, Lago Pueyrredón, La Cueva, Río Shehuén; Santa Cruz Province. Santa Cruz Fm.

Psilopterus minutus (Ameghino 1891)

LOCALITY AND HORIZON: Monte Observación, Santa Cruz Province. Santa Cruz Fm.

Lophiornis obliquus Ameghino 1891

LOCALITY AND HORIZON: Monte Observación, Santa Cruz Province. Santa Cruz Fm.

FRIASIAN

Order Accipitriformes, Family Accipitridae:

Accipitridae genus and species indeterminate

LOCALITY AND HORIZON: Ing. Jacobacci, Neuquén Province. Unnamed formation.

REMARKS: This and the following falconid species are the first reported fossil birds from mammal-bearing Friasian sediments. The material is very fragmentary and identification beyond the family level cannot be attempted.

Family Falconidae:

Falconidae genus and species indeterminate

LOCALITY AND HORIZON: Ing. Jacobacci, Neuquén Province. Unnamed formation.

CHASICOAN

Order Ralliformes, Family Psilopteridae:

Psilopterus new species

LOCALITY AND HORIZON: Arroyo Chasicó, Buenos Aires Province. Vivero member of the Arroyo Chasicó Fm.

REMARKS: This species is currently being described (Tonni in press).

HUAYQUERIAN

Order Accipitriformes, Family Teratornithidae:

Teratornithidae new genus new species

LOCALITY AND HORIZON: Salinas Grandes de Hidalgo, Departamento Atreucó, La Pampa Province. Epecuén Fm.

REMARKS: This specimen is described by Campbell and Tonni, this vol.

Order Ralliformes, Family Phorusrhacidae:

Andalgalornis ferox Patterson and Kraglievich 1960

LOCALITY AND HORIZON: Chiquimil, Catamarca Province. Andalgala Fm.

Onactornis depressus Cabrera 1939

LOCALITY AND HORIZON: Lago Epecuén, Buenos Aires Province. Epecuén Fm.

Family Psilopteridae:

Procariama simplex Rovereto 1914

LOCALITY AND HORIZON: Catamarca Province. "Araucanense stage."

Hermosiornis incertus Rovereto 1914

LOCALITY AND HORIZON: Catamarca Province. "Araucanense stage."

MONTEHERMOSAN

Order Rheiformes, Family Rheidae:

Heterorhea dabbenei Rovereto 1914

LOCALITY AND HORIZON: 17 km SW of Pehuén-Có, Buenos Aires Province. Monte Hermoso Fm.

Order Tinamiformes, Family Tinamidae: *Tinamisornis parvulus* Rovereto 1914

LOCALITY AND HORIZON: 17 km SW of Pehuén-Có, Río Quequén Salado, Buenos Aires Province. Monte Hermoso Fm., "Irenense."

REMARKS: For a discussion of this and the following species of tinamous see Tonni (1977a).

Eudromia intermedia (Rovereto 1914)

LOCALITY AND HORIZON: 17 km SW of Pehuén-Có, Buenos Aires Province. Monte Hermoso Fm.

Eudromia sp.

LOCALITY AND HORIZON: Río Quequén Salado, Buenos Aires Province. "Irenense."

Order Ralliformes, Family Psilopteridae: *Prophororhacus rapax* (J. Kraglievich 1946)

LOCALITY AND HORIZON: Atlantic coast near Arroyo Lobería, Partido de Gral. Pueyrredon, Buenos Aires Province. Chapadmalal Fm.

Family Cariamidae: *Chunga incerta* Tonni 1974

LOCALITY AND HORIZON: 17 km SW of Pehuén-Có, Buenos Aires Province. Monte Hermoso Fm.

Order Accipitriformes, Family Vulturidae: *Dryornis pampeanus* Moreno and Mercerat 1891

LOCALITY AND HORIZON: 17 km SW of Pehuén-Có, Buenos Aires Province. Monte Hermoso Fm.

REMARKS: A revision of the type material resulted in the placement of this species, originally presumed to be a phorusrhacoid, in the Vulturidae, as stated by Brodkorb (1967). It is closely related to *Vultur*.

"MESOPOTAMIAN"

Order Ralliformes, Family Phorusrhacidae: *Andalgalornis steulleti* (L. Kraglievich 1931)

LOCALITY AND HORIZON: Cliffs of the Río Paraná, Entre Ríos Province. "Mesopotamian" (Basal part of the Ituzaingó Fm. of Aceñolaza (1976)).

REMARKS: For comments on this and the following two species see Patterson and Kraglievich (1960).

Andalgalornis deautieri (L. Kraglievich 1931)

LOCALITY AND HORIZON: Cliffs of the Río Paraná, Entre Ríos Province. "Mesopotamian" (Basal part of the Ituzaingó Fm. of Aceñolaza (1976)).

Onactornis? pozzi (L. Kraglievich 1931)

LOCALITY AND HORIZON: Cliffs of the Río Paraná, Entre Ríos Province. "Mesopotamian" (Basal part of the Ituzaingó Fm. of Aceñolaza (1976)).

ENSENADAN

Order Tinamiformes?, Family Tinamidae?: *Querandiornis romani* Rusconi 1958

LOCALITY AND HORIZON: "Toscas of the Río de la Plata," in the proximity of the Estación Anchorena, Buenos Aires Province. Ensenada Fm.

REMARKS: The type material could not be located for restudy, but some of the characters cited by Rusconi (1958) in his description of the species, e.g., foramen magnum pyriform and skull globular, make its taxonomic position questionable. He compared the material, a skull, with two living species, *Eudromia elegans* and *Fulica leucoptera,* finding similarities and differences that are not only non-diagnostic, but so general that they could be applied to the description of the skull of almost any living bird. In his description Rusconi himself expressed doubts as to whether he should place the fossil in the Tinamiformes, or in the Ralliformes; he felt "inclined" to place it in the Tinamidae.

Order Rheiformes, Family Rheidae: *Rhea anchorenensis* (C. Ameghino and Rusconi 1932)

LOCALITY AND HORIZON: "Reefs of the Río de la Plata opposite the Estación Anchorena," Buenos Aires Province. Ensenada Fm.

REMARKS: Brodkorb (1963) established *Rhea americana anchorenense* C. Ameghino and Rusconi as a separate species, *R. anchorenensis*. A re-evaluation of the holotype verifies this assignment.

Order Anseriformes, Family Anatidae: *Anas leucophrys* Vieillot 1816

LOCALITY AND HORIZON: Partido de Gral. Alvarado, Buenos Aires Province. Miramar Fm.

REMARKS: See Tonni (1969) for a report on the occurrence of this species.

Order Psittaciformes, Family Psittacidae: *Cyanoliseus ensenadensis* (Cattoi 1957)

LOCALITY AND HORIZON: Olivos, Buenos Aires Province. Ensenada Fm.

REMARKS: For comments on this species see Tonni (1972).

Order Passeriformes, Family Furnariidae: *Cinclodes major* Tonni 1977

LOCALITY AND HORIZON: Mar del Plata, Buenos Aires Province. Miramar Fm.

Family Emberizidae: *Zonotrichia robusta* Tonni 1970

LOCALITY AND HORIZON: Miramar, Buenos Aires Province. Miramar Fm.

Sicalis sp.

LOCALITY AND HORIZON: Mar del Plata, Buenos Aires Province. Miramar Fm.

REMARKS: Material referable to this genus was studied by Tonni (1973). The size of this specimen must have been similar to that of the living species *Sicalis olivascens* or *S. auriventris*.

Because of the poor representation of the material it was not given a specific assignation. It is, to the present, the oldest record for the genus.

LUJANIAN

Order Tinamiformes, Family Tinamidae: *Nothura paludosa* Mercerat 1897

LOCALITY AND HORIZON: Arrecifes, Buenos Aires Province. Buenos Aires Fm.

REMARKS: This species, like others described by Mercerat, was not adequately described or figured. As in other instances, a re-evaluation of the type was not possible because it could not be located.

Order Rheiformes, Family Rheidae: *Pterocnemia fossilis* Ameghino 1882

LOCALITY AND HORIZON: Olivera, Buenos Aires Province. Buenos Aires Fm.

REMARKS: *Rhea pampeana* Moreno and Mercerat 1891 is a synonym of *Pterocnemia fossilis* Ameghino.

Rhea azarae (Moreno and Mercerat 1891)

LOCALITY AND HORIZON: Monte Hermoso, Buenos Aires Province. "Pampeano."

REMARKS: The incomplete femur on which Moreno and Mercerat founded *Protorhea azarae* is assignable to *Rhea,* and not to a camel, *"Auchenia lujanensis,"* as assumed by Ameghino (1891). Its placement in a species separate from *Rhea americana* is only tentative because of the fragmentary nature of the material.

Order Anseriformes, Family Anatidae: *Neochen debilis* (Ameghino 1891)

LOCALITY AND HORIZON: La Plata, Buenos Aires Province. "Belgranense stage."

Order Ralliformes, Family Rallidae?: *Euryonotus brachypterus* Mercerat 1897

LOCALITY AND HORIZON: Arrecifes, Buenos Aires Province. Buenos Aires Fm.

Euryonotos argentinus Mercerat 1897

LOCALITY AND HORIZON: Arrecifes, Buenos Aires Province. Buenos Aires Fm.

Order Charadriiformes, Family Laridae?: *Pseudosterna degener* Mercerat 1897

LOCALITY AND HORIZON: Luján, Buenos Aires Province. Luján Fm.

Pseudosterna pampeana Mercerat 1897

LOCALITY AND HORIZON: Arrecifes, Buenos Aires Province, Buenos Aires Fm.

Order Accipitriformes, Family Falconidae: *Lagopterus minutus* Moreno and Mercerat 1891

LOCALITY AND HORIZON: Luján, Buenos Aires Province. Buenos Aires Fm.

REMARKS: The holotype of this species, which should have been in the collections of the Museo de la Plata, could not be found. The figure given by the authors is unclear, but the specimen could probably be assigned to *Polyborus*.

Order Pelecaniformes, Family Phalacrocoracidae: *Phalacrocorax brasilianus* (Gmelin)

LOCALITY AND HORIZON: Luján, Buenos Aires Province.

REMARKS: Moreno and Mercerat (1891) named *Phalacrocorax pampeanus* on the basis of an incomplete humerus, which was actually a specimen of *P. brasilianus* (Gmelin).

RECENT

The sediments named "lacustrine post-pampean" by Ameghino (1898), or "platense stage" by Ameghino (1898) and Doering (1882), were assigned, even in recent works, to the Pleistocene, following the scheme used by Ameghino throughout his works. But these sediments, at least those from typical localities from which bird remains were collected, e.g., Cañada de Rocha, Luján, and Mercedes, are actually post-Pleistocene in age. The sediments of the "platense stage" were deposited in enclosed basins and flood plains as lentic and lotic deposits in Buenos Aires Province, and no extinct megafauna has ever been recovered from them. All the species recovered as fossils belong to the Recent indigenous fauna of the area. With reference to the birds, even Ameghino (1898) pointed out that their remains are identical to those of Recent species. The following species are all from these deposits.

Sarcoramphus fossilis Moreno and Mercerat 1891 and *Cathartes fossilis* Moreno and Mercerat 1891 were correctly assigned to *Vultur gryphus* Linnaeus and *Cathartes aura* Linnaeus by Ameghino (1891). The assignment of *Sarcoramphus fossilis* to *S. papa* by Brodkorb (1963:257) is incorrect.

Foetopterus ambiguus Moreno and Mercerat 1891 was assigned to *Chloephaga picta* Gmelin by Tonni (1970).

Rhea fossilis Moreno and Mercerat 1891 is assignable to *R. americana,* as stated by Ameghino (1891) and verified by Brodkorb (1963:201). *Rhea subpampeana* Moreno and Mercerat 1891 is also assignable to *R. americana*.

DISCUSSION

SPHENISCIFORMES. The penguins from the "Patagoniano" comprise nine species distributed in four genera. Of the nine species, seven are found in deposits of similar age (late Oligocene–early Miocene) and in the same locality (lower course of the Río Chubut between Gaiman and Trelew). According to Simspon (1972), this is the greatest known diversity of penguins for a restricted area and geologic age, including the present.

The numerous new collections obtained by the Museo de La Plata in recent years have partially verified Simpson's (1972) hypothesis that the larger-sized species like *Arthrodytes grandis* and *Paraptenodytes brodkorbi* are found in more southerly deposits (San Julián), whereas those of smaller size come from more northerly deposits (Gaiman, Trelew). An exception to this is a record of *Paraptenodytes robustus* from Gaiman. *Palaeospheniscus gracilis* appears to be represented exclusively in those sediments of the "Patagoniano" immediately overlying the contact with the Colhué-Huapí Fm. in the lower course of the Río Chubut, in association with *Lamna cattica totuserrata* (Chondrichthyes: Isuridae) which is very abundant in the same levels, but which totally disappears 20 to 40 m above the above-mentioned contact.

RHEIFORMES. *Opistodactylus patagonicus* Ameghino 1895, from the early Miocene (Santacruzian) of Patagonia, is the first record of the order Rheiformes. Patterson and Kraglievich (1960) correctly assigned this species to the Rheidae. One record of a Recent genus is represented in the middle Pleistocene (Ensenadan) of Buenos Aires Province, while fossils of Recent species have been found in late Pleistocene (Lujanian) deposits of the same area. All known fossil rheas have been found within the present area of distribution of the family.

TINAMIFORMES. The first representatives of this order are found in Pliocene (Montehermosan) sediments of Buenos Aires Province. Two living genera, *Eudromia* and *Nothura,* are reported from these deposits, and perhaps also the Recent species *Nothura maculosa* (see Tonni 1977a).

PROCELLARIIFORMES. *Argyrodyptes microtarsus* Ameghino 1905, from marine sediments of the "Patagoniano," was described by Ameghino as a species of penguin. Simpson (1946) doubted that the species could be assigned to the Spheniscidae, and demonstrated its probable relationships with the Procellariiformes. Brodkorb (1963) correctly concluded that *A. microtarsus* belonged to the Procellariidae, a fact corroborated by Tonni (in press).

The Procellariidae are well represented in the early and middle Miocene of North America and Europe, but *Argyrodyptes microtarsus* is the only fossil record of the family for South America.

PELECANIFORMES. *Cladornis pachypus* Ameghino 1895, from lower Oligocene (Deseadan) sediments of Santa Cruz Province, is the first record for the order in South America. Wetmore (1960) placed this species in a new suborder, Cladornithes, that would also include *Cyphornis magnus* Cope 1894 and *Palaeochenoides mioceanus* Shufeldt 1916, both from the early Miocene of North America.

Liptornis hesternus Ameghino 1895, of the early Miocene (Santacruzian) of Santa Cruz Province, represents, together with *Pelecanus gracilis* Milne-Edwards 1863 from the early Miocene of Europe, the oldest record for the Pelecanidae. This family is now comprised of only one genus, *Pelecanus,* that is widely distributed in almost all tropical and warm temperate areas of the world. Over a dozen extinct species are known, all but *Liptornis hesternus* referred to *Pelecanus*.

The only records of the Phalacrocoracidae in South America are the reports of the Recent *Phalacrocorax brasilianus* in late Pleistocene deposits of Argentina (Buenos Aires Province) and Brazil, and *P. olivaceus* and *P. bougainvillii* in late Pleistocene deposits of Peru (Campbell 1979).

PHOENICOPTERIFORMES. The order Phoenicopteriformes is represented by two species of the extinct family Presbyornithidae, *Presbyornis antiquus* (Howard 1955) and *P. pervetus* Wetmore 1926 from the early Eocene (Casamayoran) of Chubut Province. *P. pervetus* has also been reported for deposits of a similar age in North America.

ARDEIFORMES. *Ciconiopsis antartica* Ameghino (1899, from lower Oligocene (Deseadan) deposits of Santa Cruz Province, is the oldest record of the Ciconiidae for the Americas, and for the world as well since this family is recorded for the first time in the Old World (Europe) inthe late Eocene–early Oligocene.

Protibis cnemialis Ameghino 1891, from the early Miocene (Santacruzian) of Patagonia, is also the oldest record of the Plataleidae for the Americas.

ANSERIFORMES. The position of *Teleornis impressus* Ameghino 1899 and *Loxornis clivus* Ameghino 1895 within this order is uncertain. Species undoubtedly belonging to the Anatidae are recorded from the early Miocene (Santacruzian) with the appearance of *Eoneornis australis* Ameghino 1895 and *Eutelornis patagonicus* Ameghino 1895, and earlier in the marine sediments of the "Patagoniano" (late Oligocene–early Miocene) where an extinct species with affinities with the Tachyerini has been found (Tonni in press). Neospecies have been recorded from middle Pleistocene deposits onward in Buenos Aires Province (Tonni 1969).

ACCIPITRIFORMES. *Cruschedula revola* Ameghino 1899 and *Climacarthrus incompletus* Ameghino 1899 are both based on non-diagnostic material and their position within the order is uncertain, but their assignment to the Accipitridae seems reasonable. Undoubted members of the Accipitridae are reported for the Santacruzian, with the appearance of *Thegornis musculosus* Ameghino 1895 and *T. debilis* Ameghino 1895. *Badiostes patagonicus* Ameghino 1895 is also from Santacruzian deposits.

The first records of these birds of prey coincides with those of the caviomorph rodents, during the early Oligocene (Deseadan). In the Miocene (Santacruzian and Friasian), such rodents and other small rodent-like mammals, e.g., the Interatheriidae and Hegetotheriidae, acquire a great species diversity and population density, coinciding with a notable increase in the number of accipitriforms represented during the Friasian (in addition to those listed above, two or three species have been collected but have yet to be studied).

GALLIFORMES. *Anisolornis excavatus* Ameghino 1891, from the early Miocene (Santacruzian) of Patagonia, is the oldest record for the Cracidae in South America. The family is at present restricted to the warm forested areas of the Neotropical Region. Only a few fossils, all attributed to neospecies, are known from the late Pleistocene (Brazil, Peru), so their evolutionary history is almost totally unknown.

OPISTHOCOMIFORMES. This order is represented in the early Eocene (Casamayoran) of Patagonia by *Onychopteryx simpsoni* Cracraft 1971. The ecological requirements of this species seem to have been similar to those of the living representatives of the order, as suggested by the presence of other faunistic indicators, e.g., Leptodactylidae, Alligatoridae, and Boidae. During the early Eocene a fauna evolved in Patagonia under conditions of relatively high temperature and humidity, along with a shrubby or grassy steppe vegetation (indicated by the presence of grazing mammals) and isolated forests.

RALLIFORMES. This is the best represented avian order, both in terms of diversity and number of specimens, of the Cenozoic of Argentina. At the present, numerous species distributed in six families live in South America. In Tertiary sediments dating from the early Eocene of Chubut Province (materials from Cañadón Hondo are still being studied) are found representatives of five other, extinct, families. These five families, generally called "Phorusrhacoids," differentiated into several different adaptive types, such as cursorial predators

(Phorusrhacidae), graviportal scavengers (Brontornithidae), and cursorial predators capable of limited flight (Psilopteridae).

In the Deseadan sediments of Patagonia three of the extinct families are represented: Phorusrhacidae, Brontornithidae, and Psilopteridae. A species of the Cariamidae, *Riacama caliginea* Ameghino 1899, is recorded for the first time. This family is restricted to South America, being represented at the present time by two monotypic genera, *Cariama* Brisson and *Chunga* Hartlaub. A new species of *Chunga* is currently being described from Montehermosan sediments of Buenos Aires Province.

Cunampaia simplex Rusconi 1946 is recorded from the late Eocene–early Oligocene of Mendoza Province. It represents a monotypic family of questionable taxonomic position.

During the Santacruzian the large phorusrhacoids reach their greatest diversity. At this time there existed representatives of four families: the three mentioned above for the Deseadan, and the Palaeociconiidae. The decline of this group, both in numbers and diversity, began before the end of this period. During the Huayquerian, only the Phorusrhacidae and Psilopteridae are present, represented by a total of four species. In Montehermosan deposits there are also records of the last two mentioned families, but the number of specimens found in well-known localities is low. There are no records of these large ralliforms in Uquian deposits.

The oldest record for the family Aramidae is *Aminornis excavatus* Ameghino 1899, from the early Oligocene of Santa Cruz Province. *Loncornis erectus* Ameghino 1899, from the same locality and horizon, is placed with doubt in that family by Brodkorb (1967).

Euryonotus brachypterus Mercerat 1897 and *E. argentinus* Mercerat 1897 were placed in the Rallidae by Mercerat. The type material could not be located and the descriptions are too brief to enable verification of that assignment. These fossils came from late Pleistocene deposits of Buenos Aires Province.

CHARADRIIFORMES. The Laridae are represented in the late Pleistocene of Buenos Aires Province by two presumed extinct species: *Pseudosterna degener* Mercerat 1897 and *P. pampeana* Mercerat 1897. But, as with the case with the rallids described by Mercerat, their taxonomic position is very doubtful.

PSITTACIFORMES. One extinct species of the Psittacidae, *Cyanoliseus ensenadensis* (Cattoi 1957), is known from Argentina (middle Pleistocene of Buenos Aires Province). The living species *C. patagonus* was present in the late Pleistocene of Argentina (Buenos Aires Province).

PASSERIFORMES. The Furnariidae are represented by an extinct species of *Cinclodes, C. major* Tonni 1977, from the Ensenadan of Buenos Aires Province. *C. major* shows a degree of specialization similar to that of *C. patagonicus* (Gmelin).

The only other family of this order unquestionably represented in Cenozoic sediments of Argentina is the Emberizidae, of which one extinct species, *Zonotrichia robusta* Tonni 1969, and one undetermined species of *Sicalis* are known. Both are from middle Pleistocene deposits of Buenos Aires Province.

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A THICK-KNEE (AVES: BURHINIDAE) FROM THE PLEISTOCENE OF NORTH AMERICA, AND ITS BEARING ON ICE AGE CLIMATES

By Alan Feduccia[1]

ABSTRACT: A new species of thick-knee (Aves: Burhinidae) from the Pleistocene (Sangamon) of North America (Decatur County, Kansas) is described; it is named *Burhinus aquilonaris* new species. The genus *Burhinus* is a good indicator of dry, tropical savannah, and its presence in Kansas during the Sangamon is evidence that similar habitat existed in the High Plains at that time.

The late Professor Claude W. Hibbard of the University of Michigan amassed an exceptionally large collection of fossil birds in his quest for small mammals. These avian fossils are fundamental to our understanding of the late Pliocene avifauna of North America and have been reviewed and discussed elsewhere (Feduccia 1975).

Hibbard's theories on the climates of the Pliocene and Pleistocene of North America were less than well received over the years and even now are not generally accepted; this was a constant plague to him and resulted in many heated debates. "Hibbie," as he was affectionately known, was constantly awaiting additional fossil evidence to bolster his radical views of Plio-Pleistocene climates, but unfortunately there was little among the collections of fossil birds to provide clues to paleoclimate or paleoecology. One such fossil had been sent to the late Dr. Alexander Wetmore in 1943. I have examined the considerable volume of correspondence between Hibbard and Wetmore over this specimen. This began in 1943 and in it Hibbard continually urged Wetmore to publish a description of the fossil. Wetmore was extremely busy during those years, including among his duties being Secretary of the Smithsonian Institution. The fossil concerned was a thick-knee (*Burhinus*) from the Pleistocene of North America, and Hibbard had known its generic identity since the 1940's.

In a letter from Hibbard to Wetmore in 1962, Hibbard writes: "Back in the early 40's I collected a bird humerus. . . . I sent the material to Professor Loye Miller who considered it nearest to the Thick-knees of Tropical America. He returned it due to the lack of comparative material and suggested that I send it to you, which I did immediately. . . . Over the years I have told my classes of the occurrence of a Thick-knee in the fauna of Kansas from the very late Illinoian or early Sangamon. Have I been wrong? . . . Is the specimen good enough for identification? If so, and a Thick-knee, could you possibly find time to report its occurrence. If it is such, I think it is quite important . . . ." Modern species of *Burhinus* occur only in dry, tropical savannahs, and Hibbard was most anxious to see the description appear. Over the years "Hibbie" constantly attempted to impress his students and colleagues with the importance of a Pleistocene thick-knee from North America. In an effort to complete some of Dr. Wetmore's unfinished work, the now famous thick-knee is here described. Wetmore left an incomplete description of this fossil and the name used here is that which he had chosen for it.

SYSTEMATICS

Order Charadriiformes

Family Burhinidae

Burhinus aquilonaris new species

Figure 1

HOLOTYPE: Left humerus (complete except for minor breakage in middle of outer margin of deltoid crest), University of Kansas Museum of Natural History, Vertebrate Paleontology No. 6822. Collected in August 1943, by C.W. Hibbard.

LOCALITY AND HORIZON: From the late Pleistocene (Sangamon) Sanborn Formation, bed No. 2, at level of highway culvert in bottom of draw on south side of Route U.S. 36, in NE ¼, Sec. 3, T.3, R.27W., Decatur County, Kansas. The holotype was mentioned specifically in an early report by Hibbard et al. (1944), who, in listing a jaw fragment of a prairie dog, *Cynomys ludovicianus* (Ord), "collected 6 feet [~1.8 m] below the soil zone in bed 2 at locality no. 10," remarked that "the remains of a bird (KUMVP No. 6822) . . . were found associated" with it.

MEASUREMENTS OF HOLOTYPE (in mm): Length 88.2; transverse width of shaft at center 5.2; transverse width across distal end 13.2.

ASSOCIATED PARATYPES (probably from same individual): A nearly complete left radius, the proximal and distal portions of a left ulna, three rib fragments, and a fragmented left ilium, same data and catalog number as holotype. These

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Figure 1. *Burhinus aquilonaris*, new species, holotype left humerus, University of Kansas Museum of Natural History, Vertebrate Paleontology No. 6822. From left to right, and bottom left to right: palmar, ventral, anconal, proximal, and distal views. All views ×1½.

were found associated with the holotype humerus and almost certainly belong to the same individual. The fossil radius measures 94.3 mm in total length, those of the continental races of *B. bistriatus* (Wagler), 98.0 to 119.6 mm ($\bar{x} = 109.6$, s.d. = 7.3, n = 13); of *B. b. dominicensis* (Cory), 91.9–92.9 mm; and of *B. superciliaris* (Tschudi), 87.7 and 94.2 mm.

ETYMOLOGY: Latin, *aquilonaris*, meaning northern or northerly.

DIAGNOSIS: Intermediate in size between the continental American races of *Burhinus bistriatus* and the smaller *Burhinus bistriatus dominicensis* of Hispaniola; slightly larger than *Burhinus superciliaris*. Fourteen specimens of humeri representing the continental races of *B. bistriatus* range from 91.0 to 103.6 ($\bar{x} = 96.8$, s.d. = 4.6) in length; three specimens of *B. b. dominicensis* range from 82.2 to 84.1 mm ($\bar{x} = 83.5$, s.d. = 1.1); and two specimens of *B. superciliaris* measure 80.7 and 86.9 mm. Closest in characters to the living continental races of *B. bistriatus,* but differs in having (1) deltoid crest slightly longer; (2) bicipital furrow smoother, without definite depression at proximal end below head found in modern forms; (3) outline of head more angular, less smoothly rounded; (4) internal tuberosity slightly heavier; (5) ectepicondylar prominence with proximal external margin more angular; (6) entepicondyle more produced distally and more angular, with distal margin extending to level of distal margin of trochlea; and (7) brachial depression more sharply marked, with the impression of M. brachialis anticus more clearly defined.

REMARKS: The only record of an extinct species of *Burhinus* is that of *Burhinus nanus* Brodkorb (1959), described from Upper Pleistocene cave deposits on New Providence Island, Bahamas. This species, based on a left coracoid, is distinguished from modern *Burhinus bistriatus dominicensis* of Hispaniola by smaller size.

In addition, *Burhinus superciliaris,* a small South American burhinid that is common in semi-arid regions of northwestern South America (extending to northern Chile) is known as a fossil from the late Pleistocene of southwestern Ecuador, and from the late Pleistocene Talara Tar Seeps in northwestern Peru (Campbell 1976, 1979). A larger American burhinid, *Burhinus bistriatus,* that is known in arid regions from northern South America northward into southeastern Mexico, is not definitely recorded in the fossil record, but Howard (1971) has reported burhinid fossils from the Pleistocene of Eddy County, New Mexico, and from San Josecito Cave in northeastern Mexico as approximating the living *B. bistriatus* in size.

HIBBARD'S INTERPRETATION OF PLIOCENE AND PLEISTOCENE CLIMATES

Hibbard was greatly impressed with the presence of large land tortoises (*Geochelone*) in North America during the Pliocene and Pleistocene. In a now classic paper (Hibbard 1960), he outlined a general climatic interpretation based on the assumption that the overall physiology of large tortoises did not differ significantly from that of the living species now restricted to the Galapagos Islands, South America, Africa, Madagascar and other islands of the Indian Ocean, Ceylon, India, and southeastern Asia.

There is considerable dispute as to what constitutes the end of the Upper Pliocene and the beginning of the Pleistocene, a time that falls within a North American land mammal age, the Blancan. The reason for this is that the first Pleistocene fauna was also the last Pliocene fauna. In addition, there was no boreal fauna (as at present) to be shifted southward with the southward movement of the first continental glacier and provide a paleontological indication of the onset of glaciation. Nonetheless, Hibbard considered the very large, thick-shelled land tortoise, *Geochelone rexroadensis* (Oelrich 1952), found in association with a smaller tortoise, *G. turgida* (Oelrich 1957), in the Rexroad Formation, to indicate an equable climate in Kansas in the Blancan, a climate in which freezing conditions did not exist. As he stated (Hibbard 1960:17), "It is not known how far north the large tortoises ranged during the Upper Pliocene, but it can be assumed that part of the Upper Pliocene was as equable as the climate during part of the first interglacial which allowed these large tortoises to live as far north as Brown County, Nebraska (McGrew 1944:48–49)." It seemed clear to Hibbard that there was no evidence to indicate that, "Conditions essentially the same as those of the present were reached by the Upper Pliocene . . . but the outbreaks of polar air so characteristic of the present winters appear to be a development of the late Pliocene" (MacGinitie 1958:70–71).

Faunas of the first glacial, or Nebraskan, are not well known, and no fauna has been found that would have been characteristic of the maximum extent of continental glacial advance. However, immediately prior to the Nebraskan, the giant land tortoises are known from the High Plains region as far north as northern Nebraska (Sand Draw Locality—see Zakrzewski 1975 for age), and parts of a large tortoise have been found in deposits of the first interglacial (Aftonian) in Meade County, Kansas (Deer Park local fauna). The pygal scute of a tortoise from Nebraska represents a specimen of approximately 2 m length (McGrew 1944). Hibbard (1960:19) concluded that, "These large tortoises lived in a subtropical climate . . . ." In addition, the occurrence of a large, thick-shelled *Geochelone* from the Aftonian Borchers local fauna of Meade County, Kansas (above the Pearlette ash—see Zakrzewski 1975), indicated to Hibbard (1960:21), "a subtropical climate with winter temperatures not lower than 32°F [0°C]." Even during the second glacial, the Kansan, remains of a large, thick-shelled *Geochelone* (estimated length, 2 m) are known from the Seymour Formation of northern Texas below the Pearlette ash, in association with remains of alligator, glyptodonts, a giant armadillo, ground sloths, *Stegomastodon,* mammoths, tapirs, horses, and a leptodactylid frog. This association indicated to Hibbard that in Texas during the late Kansan the winters must have been considerably warmer than at present. By the Illinoian, or third glacial period, the High Plains faunas take on an aspect of a more northern Recent fauna than those of either the Nebraskan or Kansan. But even in the third interglacial, or Sangamon, the large tortoises (*Geochelone*) appear again in southwestern Kansas (Cragin Quarry local fauna). These indicated to Hibbard that during the Sangamon there existed in southwestern Kansas subtropical conditions with winter temperatures seldom or never lower than 0°C. The last glacial, or Wisconsin, period is characterized by the massive extinctions of the vertebrate fauna that characterized the end of the Pleistocene of North America. Even the giant tortoises that had been present continuously in Florida throughout the Pleistocene became extinct. These extinctions, which began approximately 12,000 years ago, are attributed by Martin (1958 and numerous subsequent papers) to man rather than climatic change, but Grayson (1977) has pointed out that birds and mammals underwent comparable amounts of generic extinction. The magnitude of avian extinctions (at the same time as the mammalian extinctions) is incompatible with Martin's "Pleistocene Overkill Hypothesis." This evidence would, of course, lend support to Hibbard's view that the harsh climate and associated climatic zoning of Recent times was a consequence of the Wisconsin glaciation. This view probably also explains the massive Pleistocene extinctions without the intervention of man.

BURHINUS IN THE PLEISTOCENE OF NORTH AMERICA

Hibbard was extremely anxious for avian paleontologists to describe the fossil birds that he had discovered, but as the descriptions emerged there was little in the way of avian indicators of climatic conditions in the Pleistocene. Collins (1964) had identified some of the ibis bones as belonging to taxa now confined to the Neotropics, but the bone fragments used in his identifications are unidentifiable (Feduccia 1975). *Burhinus aquilonaris* represents the first of Hibbard's avian fossils to clearly indicate something of the Pleistocene paleoclimate and paleoecology of the High Plains. The various species of thick-knees (Burhinidae) are widespread in tropical regions of the

Old World. In the New World, the genus *Burhinus* is at present confined to Hispaniola and arid portions of the mainland from southern Mexico to Peru and Brazil. The genus is characteristic of dry, scrubby, open country. Slud (1964:102) states that in Costa Rica *Burhinus bistriatus* is "an indicator species of the scrubby . . . cattle country, frequents openings in bushy and thickety growth amid low woodland as well as open ranges and coastal grassy 'plains' akin to salt marshes. A terrestrial bird, occurring singly or in small groups, it is both diurnal and nocturnal." Slud's description is typical for the American species of *Burhinus,* and can be reasonably extended to characterize the Pleistocene species as well. The species of *Burhinus* are thus good indicators of tropical, dry savannah, and we can assume this to have been the habitat in Decatur County, Kansas, during the Sangamon when *Burhinus aquilonaris* lived there.

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A REVIEW OF THE RANCHOLABREAN AVIFAUNA OF THE ITCHTUCKNEE RIVER, FLORIDA

By Kenneth E. Campbell, Jr.[1]

ABSTRACT: A collection of 1363 fossil bird bones representing 56 species is described, bringing the known avifauna from the late Pleistocene (Rancholabrean) deposits of the Itchtucknee River, Florida, to 67 species represented by over 1750 specimens. A predominance of aquatic species indicates the presence of extensive freshwater pond and marsh habitat. A mid-Wisconsinan age, or younger, is suggested for the deposits. The recognition of a paleospecies of *Milvago* (Accipitriformes: Falconidae) in Florida marks the first record of the genus for North America.

The Itchtucknee River, located in Columbia County, Florida, has long been known as a rich source of Pleistocene fossils, including mammals (Simpson 1929, 1930, 1932; Kurtén 1965; Martin 1969), reptiles (Auffenberg 1963), and birds (Wetmore 1931; McCoy 1963).

In the years subsequent to McCoy's report on the paleoavifauna, over 1300 additional specimens of fossil birds have been recovered from the Itchtucknee River by numerous collectors; these form the basis for the present paper. Fossils from the Itchtucknee River are generally found as stream float along the bottom of the river, but they may also be collected as they wash out of the deposits. The avian fossils reported here were collected from a number of sites. Although the locality is given as simply "Itchtucknee River," some specimens have more specific locality data. The specimens reported below are part of the collections of the Florida State Museum, University of Florida.

As discussed by McCoy (1963), the Itchtucknee River is considered a Pleistocene, possibly mid-Wisconsinan, locality. Webb (1974) lists it among the Rancholabrean sites of Florida based on the mammalian taxa contained therein. The exact age of most of the specimens reported here cannot be determined because the river is eroding deposits of probably different ages, and often redepositing fossils on younger sediments. Fossils of different ages are often mixed on the river bottom. Also, because the river meanders in places, the processes of erosion and redeposition continued over time have resulted in deposits containing fossils of mixed ages; these are now being exposed on the bottom of the river once again. I do not believe any of the fossils are older than Rancholabrean, but because of the mixing action of the river there may be a few post-Rancholabrean fossils inadvertently included. Comments by McCoy (1963) as to the type of preservation of the fossil materials and the nature of the river and specific sites are still pertinent and will not be repeated here.

The following faunal list includes only those specimens I identified; the fossils identified by McCoy are listed in Table 1. Many of the specimens identified by McCoy (1963) have been rechecked, either by myself or others, resulting in the correction of some misidentifications (see Table 1). A check of all McCoy's identifications would be very difficult because he reported on fossils from four different collections and did not give catalog numbers of most of the specimens he listed.

FAUNAL LIST

Podilymbus podiceps (Linnaeus 1758)
Pied-billed Grebe

MATERIAL: Coracoids (19); humeri (55); ulnae (7); carpometacarpi (2); femora (17); tibiotarsi (22); tarsometatarsi (31). UF/FSM 15209–15213, 15215–15219, 15221–15222, 15224–15324, 22305–22341.

REMARKS: Storer (1976) studied most of the material listed above for his report on Pleistocene Pied-billed Grebes. I concur with his conclusion that *P. magnus* should be regarded as a synonym of *P. podiceps*.

Podilymbus wetmorei Storer 1976

MATERIAL: Two complete left femora, 1 complete left tarsometatarsus. UF/FSM 15214, 15220, 15223.

REMARKS: Storer (1976) referred these specimens to *P. wetmorei* in his original description of that species on the grounds that the femora are much heavier and the tarsometatarsus is much thicker than those of *P. podiceps.* Although I agree with Storer that the specimens referred to *P. wetmorei* are significantly larger than corresponding bones of *P. podiceps,* I think there is a good possibility that the former may have been a resident race of *P. podiceps* in peninsular Florida during the Pleistocene. The type locality for *P. wetmorei* is the Dixie Lime Products quarry, Locality IA, 1.6 km south of Reddick, Marion County, Florida. The lack of any good osteological characters other than size that separate *P. podiceps* and *P. wetmorei* might be taken as evidence for this possibility.

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[1] Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, CA 90007.

Contrib. Sci. Natur. Hist. Mus. Los Angeles County. 1980. **330:**119–129.

Table 1. Avian species from the late Pleistocene deposits of the Itchtucknee River, Florida.

	(From McCoy 1963)		Added		Total	
Species	Number of Specimens	Minimum Number of Individuals	Number of Specimens	Minimum Number of Individuals	Number of Specimens	Minimum Number of Individuals
Podilymbus podiceps	60[1]	4	150	27	210	31*
†*Podilymbus wetmorei*	0	0	3	2	3	2
Podiceps auritus	1	1	0	0	1	1
Phalacrocorax auritus	21	3	74	9	95	12*
Anhinga anhinga	1	1	3	2	4	2
Ardea herodias	8	2	39	8	47	8
Casmerodius albus	0[2]	0	1	1	1	1
Butorides virescens	1	1	0	0	1	1
Egretta caerulea	1[3]	1	1	1	2	2*
Nycticorax nycticorax	2	1	4	1	6	2*
Botaurus lentiginosus	2[4]	1	3	1	5	1
†*Ciconia maltha*	2	1	9	2	11	2
Mycteria americana	0[5]	0	3	1	3	1
Eudocimus albus	1	1	0	0	1	1
Olor columbianus	1	1	9	4	10	4
Olor buccinator	15	5	47	5	62	5
Branta canadensis	25[6]	4	83	9	108	9
Anas platyrhynchos	19[7]	3	144	24	163	24
Anas rubripes	6	2	10	4	16	6
Anas acuta	6	2	25	4	31	5
Anas discors	16	6	30	9	46	9
†*Anas itchtucknee*	1	1	0	0	1	1
Anas crecca	3	1	4	2	7	2
Anas strepera	4	1	11	4	15	4
Anas americana	5	4	3	1	8	4
Anas clypeata	5	2	32	8	37	9
Aix sponsa	9	3	27	7	36	8*
Aythya affinis	17	4	40	14	57	17*
Aythya collaris	25	10	115	22	140	32*
Aythya americana	2	1	2	1	4	2
Aythya valisineria	16	4	95	15	111	15
Bucephala clangula	0	0	3	2	3	2
Bucephala albeola	1	1	0	0	1	1
Lophodytes cucullatus	4	2	12	5	16	8*
Mergus merganser	1	1	0	0	1	1
Mergus serrator	0	0	1	1	1	1
Oxyura jamaicensis	0	0	5	1	5	1
Cathartes aura	0	0	2	1	2	1
Coragyps atratus	1	1	1	1	2	1
†*Gymnogyps amplus*	1	1	0	0	1	1
Accipitridae gen. et sp. indet.	1[8]	1	1	1	2	1
Buteo lineatus	0	0	3	1	3	1
Buteo jamaicensis	1	1	6	3	7	3
Haliaetus leucocephalus	0	0	3	2	3	2
†*Milvago readei*	0	0	2	1	2	1
Pandion haliaetus	10	3	15	5	25	6*
Colinus virginianus	0	0	4	1	4	1
Meleagris gallopavo	27	9	141	18	168	23*
Grus americana	3	1	16	3	19	3
Grus canadensis	0	0	3	1	3	1
Aramus guarana	0	0	4	1	4	1
Rallus elegans	2	1	4	1	6	2*
Rallus limicola	1	1	0	0	1	1
Porzana carolina	1	1	1	1	2	1
Gallinula chloropus	15	3	63	7	78	7
†*Gallinula brodkorbi*	5	3	29	5	34	5
Porphyrula martinica	0	0	7	3	7	3
Fulica americana	38[9]	11	55	16	93	27
†*Ectopistes migratorius*	0	0	1	1	1	1
Zenaidura macroura	0	0	1	1	1	1
Tyto alba	1[10]	1	1	1	2	1
Otus asio	0	0	2	1	2	1
Strix varia	0	0	1	1	1	1
Colaptes auratus	1	1	0	0	1	1

Table 1. Continued.

Species	(From McCoy 1963)		Added		Total	
	Number of Specimens	Minimum Number of Individuals	Number of Specimens	Minimum Number of Individuals	Number of Specimens	Minimum Number of Individuals
Corvus brachyrhynchos	0	0	9	2	9	2
Agelaius phoeniceus	1	1	0	0	1	1
Quiscalus quiscula	2	1	0	0	2	1

† Extinct species.

* Approximate only. Total obtained by adding figures of McCoy with those reported on here, which will not necessarily give an accurate minimum number.

[1] Including 2 specimens listed as *Podilymbus magnus* Shufeldt. However, in his formal list McCoy stated there were 47 specimens of *P. podiceps*, not 58 as listed in his table.

[2] McCoy referred this specimen to *Casmerodius albus*.

[3] McCoy listed this species in his table, but did not include it in his faunal list.

[4] McCoy referred this specimen, a complete humerus, to *Branta canadensis*.

[5] Including two specimens referred to *Palaeophoyx columbiana* by McCoy.

[6] I have combined here the two subspecies of *Branta canadensis* listed by McCoy.

[7] Including specimens listed as *Anas fulvigula* by McCoy.

[8] McCoy referred this specimen to *Teratornis merriami*.

[9] Including specimen assigned to *Fulica minor* Shufeldt, considered a synonym of *F. americana* (Olson 1977).

[10] Including specimen referred to *Palaeophoyx columbiana* by McCoy.

Phalacrocorax auritus (Lesson 1831)
Double-crested Cormorant

MATERIAL: Maxilla; mandible; coracoids (11); scapulae (2); humeri (11); ulnae (22); radius; carpometacarpi (5); femora (4); tibiotarsi (8); tarsometatarsi (8). UF/FSM 15454–15522, 15646, 20014–20015, 22451.

Anhinga anhinga (Linnaeus 1766)
Anhinga

MATERIAL: Humerus; ulnae (2). UF/FSM 22459–22551.

Ardea herodias Linnaeus 1758
Great Blue Heron

MATERIAL: Coracoids (4); scapulae (2); humeri (3); ulnae (5); radii (2); carpometacarpi (4); femora (2); tibiotarsi (5); tarsometatarsi (12). UF/FSM 15535–15571, 20012, 22559.

Casmerodius albus (Linnaeus 1758)
Great Egret

MATERIAL: Ulna. UF/FSM 15572.

Egretta caerulea (Linnaeus 1758)
Little Blue Heron

MATERIAL: Tibiotarsus. UF/FSM 15534.

Nycticorax nycticorax (Linnaeus 1758)
Black-crowned Night-Heron

MATERIAL: Ulna; carpometacarpus; femur; tarsometatarsus. UF/FSM 15531–15533, 20013.

Botaurus lentiginosus (Rachett 1813)
American Bittern

MATERIAL: Humerus; tibiotarsus; tarsometatarsus. UF/FSM 20019, 22536–22537.

REMARKS: McCoy (1963) described a new genus and species of heron, *Paleophoyx columbiana,* from the Itchtucknee River on the basis of two coracoids and an ulna. Olson (1974) published a reappraisal of this heron, stating that he could find no characters to separate the coracoids from those of *Botaurus lentiginosus,* while the ulna represented the Barn Owl, *Tyto alba.* He stated that the coracoids fell at or slightly below (1 mm) the lower size range of Recent *B. lentiginosus,* and suggested that *B. lentiginosus* may have been smaller during the Pleistocene. The specimens listed above all fall well within the size range of Recent *B. lentiginosus,* indicating that *B. lentiginosus* was not significantly smaller during the Pleistocene.

Ciconia maltha L. Miller 1910

MATERIAL: Coracoid; scapula; humeri (2); carpometacarpus; tibiotarsi (3); tarsometatarsus. UF/FSM 1963, 15525–15530, 15591, 22555.

Mycteria americana Linnaeus 1758
American Wood-Ibis

MATERIAL: Ulna; tarsometatarsi (2). UF/FSM 15592–15594.

REMARKS: Olson (pers. comm.) has suggested that because of their large size these specimens may represent *Mycteria wetmorei* Howard.

Olor columbianus (Ord 1815)
Whistling Swan

MATERIAL: Scapula; humeri (2); ulna; femur; tarsometatarsi (4). UF/FSM 15619–15620, 15659–15663, 15665, 15668.

Olor buccinator Richardson 1831
Trumpeter Swan

MATERIAL: Cranium; coracoids (4); scapula; humeri (7); ulnae (8); radii (6); carpometacarpi (6); pelvis; femora (2); tibiotarsi (5); tarsometatarsi (5). UF/FSM 13988, 15613–15618, 15621–15658, 15666, 22449.

REMARKS: Although *Olor columbianus* has been reported as a rare winter resident in Florida (AOU 1957), *O. buccinator* is known from Florida only on the basis of fossils, and only from the Itchtucknee River (Wetmore 1931). This may suggest that the range of *O. buccinator* was shifted southward during glacial periods of the Pleistocene, and retreated northward during inter- and postglacial periods. It should be noted that there are six times as many specimens of *O. buccinator* reported here as there are of *O. columbianus*.

Branta canadensis Linnaeus 1758
Canada Goose

MATERIAL: Coracoids (16); scapulae (4); humeri (12); ulnae (16); radii (9); carpometacarpi (8); sternum; femora (5); tibiotarsi (7); tarsometatarsi (5). UF/FSM 14104, 15669–15705, 22492–22535, 22548.

Anas platyrhynchos Linnaeus 1758
Mallard

MATERIAL: Coracoids (26); scapulae (8); humeri (50); ulnae (25); radius; carpometacarpi (24); femora (2); tibiotarsi (15); tarsometatarsi (2). UF/FSM 2393, 2978, 15774–15783, 19477–19617, 22483.

REMARKS: Undoubtedly included in the material listed above are specimens of *Anas rubripes,* a species so similar osteologically to *A. platyrhynchos* that bones of the two are extemely difficult, if not impossible, to separate. If any of the material above is from *A. rubripes,* I consider specimens UF/FSM 15774–15783 to be the best possibilities.

Anas acuta Linnaeus 1758
Pintail

MATERIAL: Coracoids (7); humeri (6); ulnae (4); carpometacarpi (7); tibiotarsus. UF/FSM 15784–15808.

Anas discors Linnaeus 1766
Blue-winged Teal

MATERIAL: Coracoids (4); humeri (14); ulnae (5); carpometacarpi (4); tibiotarsi (2); tarsometatarsus. UF/FSM 15881–15910.

Anas crecca Linnaeus 1758
Green-winged Teal

MATERIAL: Humeri (4). UF/FSM 15911–15914.

Anas strepera Linnaeus 1758
Gadwall

MATERIAL: Coracoids (6); ulnae (2); carpometacarpi (3). UF/FSM 15724–15734.

Anas americana Gmelin 1789
Baldpate

MATERIAL: Coracoid; carpometacarpi (2). UF/FSM 15720–15721, 16831.

Anas clypeata Linnaeus 1758
Shoveler

MATERIAL: Coracoids (8); humeri (8); ulnae (6); carpometacarpi (10). UF/FSM 15809–15840.

Aix sponsa (Linnaeus 1758)
Wood Duck

MATERIAL: Coracoids (4); scapulae (2); humeri (12); ulnae (5); carpometacarpi (2); femur; tibiotarsus. UF/FSM 15747–15773.

Aythya affinis (Eyton 1838)
Lesser Scaup

MATERIAL: Coracoids (7); humeri (24); ulnae (3); carpometacarpi (5); tarsometatarsus. UF/FSM 15841–15880.

Aythya collaris (Donovan 1809)
Ring-necked Duck

MATERIAL: Coracoids (35); scapulae (5); humeri (52); ulnae (8); carpometacarpi (6); femur; tibiotarsi (5); tarsometatarsi (3). UF/FSM 1749, 14092, 16007–16100, 14458–14476.

Aythya americana (Eyton 1838)
Redhead

MATERIAL: Coracoid; ulna. UF/FSM 15722–15723.

Aythya valisineria (Wilson 1814)
Canvasback

MATERIAL: Crania (3); coracoids (25); scapulae (4); humeri (34); ulnae (10); carpometacarpi (12); femora (4); tibiotarsi (2); tarsometatarsus. UF/FSM 2000, 14092, 15915–16006, 22484.

Bucephala clangula (Linnaeus 1758)
Common Goldeneye

MATERIAL: Coracoid; humeri (2). UF/FSM 15716–15718.

Lophodytes cucullatus (Linnaeus 1758)
Hooded Merganser

MATERIAL: Coracoid; humeri (8); ulnae (2); femur. UF/FSM 15735–15746.

Mergus serrator Linnaeus 1758
Red-breasted Merganser

MATERIAL: Carpometacarpus. UF/FSM 15719.

Oxyura jamaicensis (Gmelin 1789)
Ruddy Duck

MATERIAL: Coracoid; humerus; ulna; tibiotarsus; tarsometatarsus. UF/FSM 15711–15715.

Cathartes aura (Linnaeus 1758)
Turkey Vulture

MATERIAL: Humerus; tibiotarsus. UF/FSM 15595, 20016.

Coragyps atratus (Bechstein 1793)
Black Vulture

MATERIAL: Tarsometatarsus. UF/FSM 20018.

Accipitridae genus and species indeterminate

MATERIAL: Proximal end of left tibiotarsus (Collection of Pierce Brodkorb No. PB 1874); distal end of left tarsometatarsus (UF/FSM 22560).

REMARKS: These specimens are from a large eagle, but they are too fragmentary to yield any diagnostic characters. They do not represent a living species, or *Amplibuteo woodwardi* (L. Miller). The tibiotarsus was referred to *Teratornis merriami* L. Miller by McCoy (1963). Olson (pers. comm.) has reported a fragmentary distal end of a tarsometatarsus (USNM 209535) from the late Pleistocene deposits of the Aucilla River, Florida, that is also from a large eagle, but it is different from the tarsometatarsus listed above. So there were at least two large, presently unknown, eagles living in Florida in the late Pleistocene.

Buteo lineatus (Gmelin 1788)
Red-shouldered Hawk

MATERIAL: Humerus; carpometacarpus; tibiotarsus. UF/FSM 22453–22454, 22491.

Buteo jamaicensis (Gmelin 1788)
Red-tailed Hawk

MATERIAL: Femur; tibiotarsus; tarsometatarsi (4). UF/FSM 15608–15612, 22452.

Haliaetus leucocephalus (Linnaeus 1766)
Bald Eagle

MATERIAL: Carpometacarpi (3). UF/FSM 22446–22448.

Genus *Milvago* Spix 1824
Milvago readei (Brodkorb 1959)

MATERIAL: Distal end and shaft of right tibiotarsus; distal end of left tarsometatarsus. UF/FSM 22561–22562. Figures 1a–c, 2b–d, 3.

REMARKS: *Milvago readei* was described by Brodkorb (1959) as a species of *Falco* on the basis of a fragmentary distal end of a left tibiotarsus (Fig. 1b, d). The type locality is Pit 2, Arredondo (Arredondo II), Alachua County, Florida. The type horizon is the Arredondo clay member of the Wicomico Formation, which Brodkorb considered to be Illinoian. In a study of the fossil box turtles (*Terrapene*) of Florida, Auffenberg (1958) also considered Arredondo II to be Illinoian, although he considered the possibility that the nearby Arredondo IA deposits might be referred to the Sangamon. Martin (1968) considered the Arredondo IA deposits to be either Illinoian, Sangamon, or Wisconsinan in age; the thrust of his paper, however, requires that the deposits be of a glacial age. No other fossils have been referred to this species since its description.

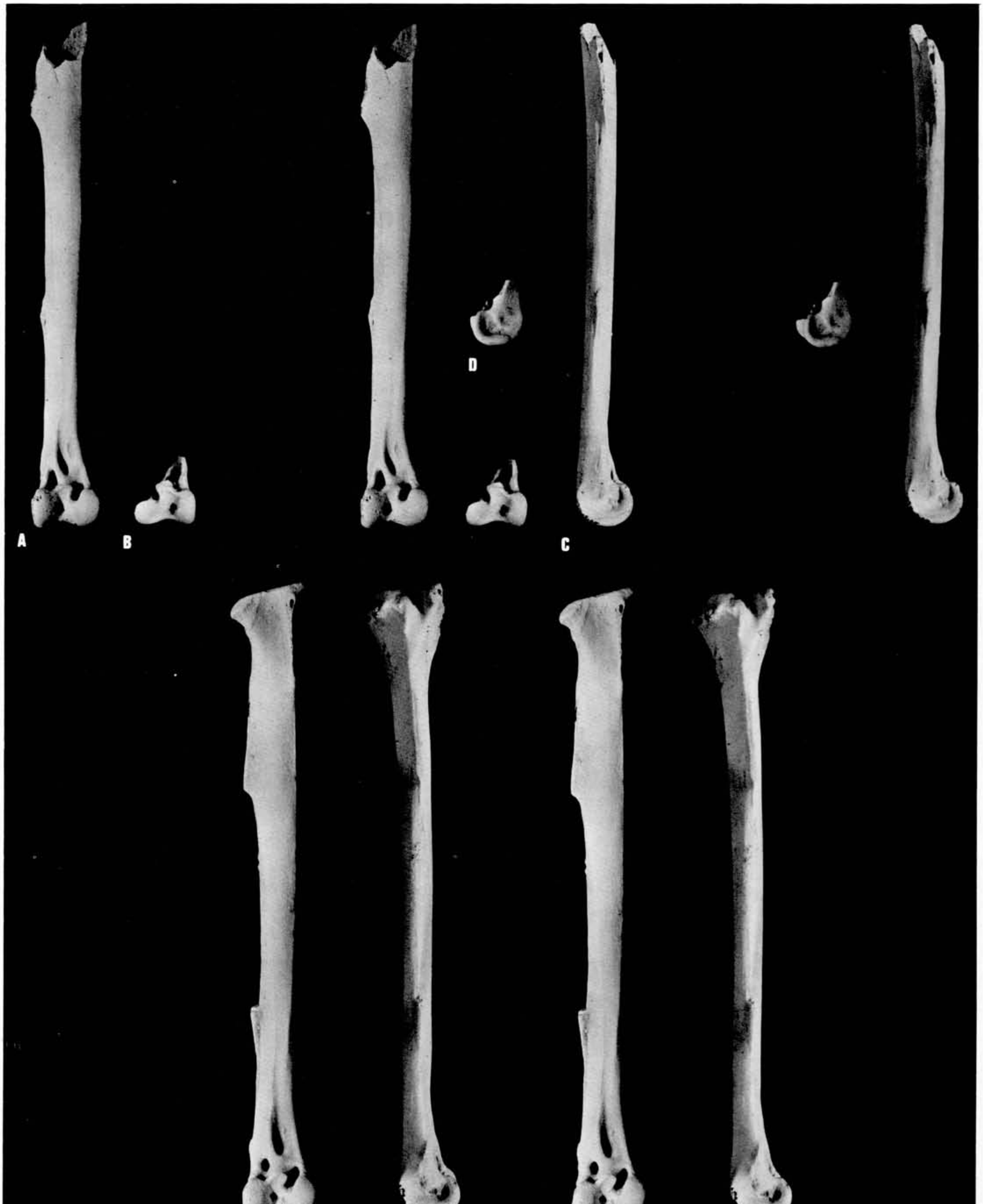
The holotype of *Milvago readei* was described as being similar to *Falco mexicanus,* but differing by having "(1) external ligamental prominence a small knob; (2) no shelf connecting external ligamental prominence and groove for peroneus profundus; (3) intercondylar pit elongated in an obliquely transverse direction toward anterior edge of external condyle; (4) size about half. Distal width, 8.0; depth of external condyle, 6.5; anterior height of external condyle, 4.7; depth of internal condyle, about 6.5 mm" (Brodkorb 1959:274–275). I consider characters (1) and (2) to be valid at the generic level, and that character (3) may also serve to separate *Falco* from *Milvago.*

The tibiotarsus from the Itchtucknee River differs from the holotype of *M. readei* in only minor details, such as having a smaller opening in the intercondylar fossa and a more prominent posteroproximal corner to the external condyle. Both of these are variable characters. The holotype tibiotarsus is slightly, but insignificantly, smaller than that from the Itchtucknee River. Measurements (in mm) of the latter are: Distal width 8.8; depth of external condyle 7.2; anterior height of external condyle 5.2; depth of internal condyle 7.3; least width of shaft 4.9. (For additional measurements of *Milvago* spp., see Olson 1976a:358; Campbell 1979:96–99.)

The Itchtucknee River tibiotarsus (Fig. 1a, c) is characterized by having the (1) external condyle with very deep concavity on external surface (moderately deep in *M. chimango* Vieillot; deep in *M. chimachima* Vieillot; similar in *M. brodkorbi* Campbell 1979); (2) internal condyle with moderate concavity on posterointernal side (shallow in *M. chimango*; deep in *M. chimachima*; similar in *M. brodkorbi*); (3) anterior intercondylar fossa with very deep pit on external side (shallow to moderately deep pit in *M. chimango* and *M. chimachima*; deep pit in *M. brodkorbi*); (4) intercondylar groove shallow in anterior view (deeper in *M. chimango, M. chimachima,* and *M. brodkorbi*); (5) external condyle deeply undercut by very large tendinal fossa (very restricted fossa in *M. chimango* and *M. chimachima*; similar in *M. brodkorbi*); (6) supratendinal bridge with proximal end positioned near external edge of shaft (positioned farther from external edge of shaft in *M. chimango, M. chimachima,* and *M. brodkorbi*); (7) shaft sturdy (similar in *M. chimango* and *M. brodkorbi*; more slender in *M. chimachima*). No tibiotarsus is known for *M. alexandri* Olson 1976.

The tarsometatarsus (Figs. 2b–d, 3) from the Itchtucknee River assigned to *M. readei* is referable to the subfamily Polyborinae on the basis of having the middle trochlea project distad much more than the inner trochlea (in the subfamily Falconinae the inner trochlea projects distad as much as or more than the middle trochlea). With the exception of *Spiziapteryx* (Olson 1976a), the species of the subfamilies Herpetotherinae (Forest Falcons) and Polihieracinae (Pigmy Falcons) have very distinctive tarsometatarsi that do not closely resemble those of the caracaras or falcons.

The tarsometatarsus agrees with that of *Milvago* and differs from those of all other genera of the subfamily Polyborinae (*Daptrius, Phalcoboenus,* and *Polyborus*) by having (1) trochleae laterally compressed; (2) middle trochlea widening markedly distad in both anterior and posterior view, and with external edge projecting more posteriad than internal edge; (3) inner trochlea not rotated or rotated slightly to moderately posteriad, with anterior surface flush with that of shaft; i.e., no point of trochlear surface extending anterior to shaft surface; (4) inner trochlea with wing (posterior projection) roughly perpendicular to long axis of shaft without turning distad at tip; (5) inner trochlea with broad flattened area on inner half of posterior side; delineated by distinct sharp edge leading from anteroproximal edge of base to tip of wing and a ridge leading from end of metatarsal facet to tip of wing.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The tarsometatarsus is characterized by having (1) inner trochlea with wing moderately large (much smaller and projecting posteriad less in *M. chimango* and *M. alexandri*; broader, but projecting posteriad less in *M. chimachima*; similar, but more massive and with only slight convexity on distal, or internal, surface in *M. brodkorbi*) (Fig. 2a, e, f); (2) inner trochlea rotated moderately posteriad (not rotated in *M. chimango, M. chimachima,* and *M. alexandri*; rotated slightly in *M. brodkorbi*); (3) internal intertrochlear notch narrow and deep (narrow and shallow in *M. chimango*; narrow and moderately deep in *M. chimachima*; moderately wide and deep in *M. alexandri*; wide and deep in *M. brodkorbi*); (4) middle trochlea with trochlear groove broad and shallow (similar, but not as broad in *M. chimango*; narrow and deeper in *M. chimachima*; similar in *M. alexandri*; similar, but slightly deeper in *M. brodkorbi*); (5) groove leading proximad from internal intertrochlear notch and skirting medial edge of metatarsal facet quite well marked; i.e., distinctly visible (slightly marked in *M. chimango, M. alexandri,* and *M. brodkorbi*; not visible in *M. chimachima*); (6) shaft broad with very pronounced ridge leading proximad from metatarsal facet (highly variable width, but only slight ridge in *M. chimango* and *M. chimachima*; slightly narrower with moderately pronounced ridge in *M. alexandri*; broader, with similar ridge in *M. brodkorbi*); (7) metatarsal facet large (smaller in *M. chimango, M. chimachima,* and *M. alexandri,* similar in *M. brodkorbi*). The tarsometatarsus is most similar in size to those of *M. chimachima,* but as the external trochlea is broken the only measurements that can be taken are as follows (in mm): Distal width (est.) 8.8; width of middle trochlea 3.4; depth of middle trochlea 4.3.

No tarsometatarsus is known for *M. readei,* but I doubt that there was more than one species in Florida at any given time during the Pleistocene. I consider referral of the tarsometatarsus to *M. readei* appropriate.

DISCUSSION: Prior to 1976 there were only two known species of *Milvago, M. chimango* and *M. chimachima,* both living in and restricted to South America, Panama, and Costa Rica. Olson (1976) described the first recognized paleospecies of *Milvago, M. alexandri,* on the basis of a complete tarsometatarsus from late Pleistocene cave deposits in Haiti, Hispaniola. Recently, I described the second known paleospecies, *M. brodkorbi,* on the basis of 160 specimens from the late Pleistocene Talara Tar Seeps of northwestern Peru (Campbell 1979). To these four species we can now add another, *M. readei,* from the late Pleistocene of Florida. This is the first record of the genus from North America. Not only is the rapid proliferation of fossil species in such a short time for a genus that previously had no fossil record remarkable, it is even more so considering that all three paleospecies have been found outside the present ranges of the living species. Also, the fact that the paleospecies are all known from late Pleistocene deposits is most interesting. Why should a genus, which appears to have been so successful, suddenly, relatively speaking, have three species in widely separated areas become extinct? Olson (1976:359) also puzzled over the lack of a clear reason for the extinction of *M. alexandri* on Hispaniola.

The proximity of *M. readei* and *M. alexandri* in time and space poses the question of whether they are both valid species, a question that becomes even stronger considering how few specimens there are for each. Based upon an examination of tibiotarsi (25) and tarsometatarsi (19) of *M. brodkorbi,* I consider intraspecific variation in *Milvago* to be relatively small. There are variable characters, but the species of *Milvago* do not appear to be nearly as variable osteologically as species of the related genus *Polyborus*. Of the seven characters listed for the tarsometatarsus, I consider the first two to be the most important. They reflect rather significant structural differences, and they varied only minimally in the sample of tarsometatarsi of *M. brodkorbi*. Although there is the possibility that larger samples would demonstrate greater variability, I consider *M. readei* and *M. alexandri* to be valid paleospecies on the basis of the currently available material.

Any speculation as to the evolution and development within the genus *Milvago* is very tenuous, based as it would be on such widely scattered data points; but a few comments can be made. Olson (1976) considered *M. alexandri* from Hispaniola more similar to *M. chimachima* than to *M. chimango,* while I considered *M. brodkorbi* from Peru to be more similar to *M. chimango* (Campbell 1979). I believe *M. readei* is more similar to *M. brodkorbi* than to either of the living species, but more similar to *M. chimachima* than *M. chimango*. There are so few comparable characters between *M. alexandri* and *M. readei* that it is impossible to suggest a similarity, or lack of same.

The living species of *Milvago* are open country, savanna, scrub forest, or forest edge inhabitants (Brown and Amadon 1968; Blake 1977). *M. chimachima* ranges from Panama and Costa Rica southward east of the Andes to northern Argentina, while *M. chimango* ranges southward from eastern Bolivia on both sides of the Andes. The two species are sympatric over a wide area of their ranges, but show no tendency to hybridize (Vuilleumier 1970). While the two species are clearly related, and some would even place them as members of a superspecies (Brown and Amadon 1968), they are quite distinct morphologically (Olson 1976).

For now it appears best to assume a South American origin for the genus, and also, to assume that habitat changes resulting from Pleistocene climatic events (Häffer 1974, 1978; Simpson and Häffer 1978; Müller 1973; Vanzolini and Williams 1970; Campbell in press) were instrumental in the speciation within this genus. *M. readei* probably extended its range into Florida via the Gulf Coast Savanna Corridor (Webb 1974) during one of the glacial periods of the Pleistocene. Florida was covered by much open savanna during dry phases of the Pleistocene when the corridor was open (Webb 1974; Watts 1971), and would have been ideal habitat for a species of *Milvago*. At the end of the Pleistocene, Florida lost most of its open country, retaining only the grasslands of the southern-

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Figure 1. Stereophotographs of tibiotarsi of *Milvago*: *Milvago readei,* referred right tibiotarsus, UF/FSM 22562, in anterior (a) and external (c) view; *Milvago readei,* holotype left tibiotarsus, PB 1632, in anterior (b) and external (d) view; *Milvago brodkorbi,* right tibiotarsus, Royal Ontario Museum ROM 17580, in anterior (e) and external (f) view. All ×1.5.

Figure 2. Stereophotographs of left tarsometatarsi of *Milvago*: *Milvago brodkorbi,* holotype, ROM 17447, in anterior (a), posterior (e), and internal (f) view; *Milvago readei,* referred, UF/FSM 22561, in anterior (b), posterior (c), and internal (d) view. All ×1.5.

most part of the state. Many other factors may have been responsible for the extinction of *M. readei,* but the climatic and vegetational changes at the end of the Pleistocene that resulted in the loss of the dry savanna habitat in Florida were probably the most important. Whether there were similar habitat changes on Hispaniola is not known at the present time. There are wide areas of xeric vegetation present on Hispaniola today (Wetmore and Swales 1931), although some of this is a result of human habitat alteration. But factors other than climate may also have played a role in the extinction of *M. alexandri.*

Pandion haliaetus (Linnaeus 1758)
Osprey

MATERIAL: Coracoids (3); ulnae (2); tibiotarsi (4); tarsometatarsi (6). UF/FSM 2725, 15596–15607, 22547, 22548.

Colinus virginianus (Linnaeus 1758)
Bobwhite

MATERIAL: Humeri (2); tibiotarsi (2). UF/FSM 15523–15524, 22455–22456.

Meleagris gallopavo Linnaeus 1758
Wild Turkey

MATERIAL: Coracoids (9); scapula; humeri (12); ulnae (11); carpometacarpi (14); sternum; pelves (2); femora (10); tibiotarsi (34); tarsometatarsi (47). UF/FSM 2069, 2332, 13988, 14104, 14126, 15328–15453, 15664, 15667, 16832, 22298–22304.

REMARKS: This series of fossils is discussed by Steadman (this vol.)

Grus americana (Linnaeus 1758)
Whooping Crane

MATERIAL: Coracoids (2); scapulae (2); ulna; radii (2); carpometacarpus; tibiotarsi (4); tarsometatarsi (4). UF/FSM 15575–15589, 22552.

Grus canadensis (Linnaeus 1758)
Sandhill Crane

MATERIAL: Ulna; radius; tarsometatarsus. UF/FSM 15590–15591, 22554.

Aramus guarauna (Linnaeus 1766)
Limpkin

MATERIAL: Humerus; tibiotarsi (3). UF/FSM 15325–15327, 20017.

Rallus elegans Audubon 1834
King Rail

MATERIAL: Coracoid; humerus; tibiotarsus; tarsometatarsus. UF/FSM 22485–22488.

Porzana carolina (Linnaeus 1758)
Sora

MATERIAL: Tibiotarsus. UF/FSM 22558.

Figure 3. Referred left tarsometatarsus of *Milvago readei,* UF/FSM 22561, in anterior, internal, and posterior view. ×2.

Gallinula chloropus (Linnaeus 1758)
Common Gallinule

MATERIAL: Coracoids (4); humeri (18); ulnae (6); carpometacarpi (5); femora (9); tibiotarsi (8); tarsometatarsi (13). UF/FSM 22371–22433.

Gallinula brodkorbi McCoy 1963

MATERIAL: Coracoids (2); humeri (3); ulnae (4); carpometacarpus; femora (7); tibiotarsi (5); tarsometatarsi (7). UF/FSM 22342–22370.

REMARKS: In a review of the Pleistocene rails of North America, Olson (1974) considered *G. brodkorbi* a valid species that was a large temporal representative of *G. chloropus.* Later, he synonymized *G. brodkorbi* with *G. chloropus* (Olson 1977), considering the former a subspecies of the latter. Both of us have examined the material from the Itchtucknee River and we agree that two forms are present, and that *G. brodkorbi* is distinguished from *G. chloropus* primarily on the basis of the larger size and greater heaviness, or stoutness, of its bones. But as Olson (1977) pointed out, the specimens McCoy (1963) referred to *G. brodkorbi* fall within the size range of Recent *G. chloropus,* possibly requiring future nomenclatural changes if no diagnostic characters other than size can be determined for the two forms when a larger series is available. Because of individual variation within gallinules I do not believe we have a sufficient number of specimens to detail specific osteological differences between the two forms.

A problem with considering *G. brodkorbi* a temporal subspecies of *G. chloropus* is that *G. chloropus* is also recognizable in the fauna and is represented by approximately twice as many specimens as *G. brodkorbi.* If one accepts the premise of Mayr (1963) that subspecies may form only if two populations of a species are isolated in space, than one must also accept the restriction that temporal subspecies must be isolated in time. Unfortunately, the specimens from the Itchtucknee River were recovered from the bottom of the river over its entire length, not in situ, so we do not know if the two forms were contemporaneous. Until further work on delineating the relationship between the two forms is possible, I prefer to maintain *G. brodkorbi* at the specific rank.

Porphyrula martinica (Linnaeus 1766)
Purple Gallinule

MATERIAL: Humeri (4); femur; tibiotarsus; tarsometatarsus. UF/FSM 20040–20043, 22434–22436.

Fulica americana Gmelin 1789
American Coot

MATERIAL: Coracoids (3); humeri (12); ulna; carpometacarpus; femora (4); tibiotarsi (28); tarsometatarsi (6). UF/FSM 20020–20039, 22437–22445, 22457–22482.

Ectopistes migratorius (Linnaeus 1766)
Passenger Pigeon

MATERIAL: Tarsometatarsus. UF/FSM 22556.

Zenaidura macroura (Linnaeus 1758)
Mourning Dove

MATERIAL: Humerus. UF/FSM 22557.

Tyto alba (Scopoli 1769)
Barn Owl

MATERIAL: Carpometacarpus. UF/FSM 15573.

Otus asio (Linnaeus 1758)
Screech Owl

MATERIAL: Humeri (2). UF/FSM 22489–22490.

Strix varia Barton 1799
Barred Owl

MATERIAL: Femur. UF/FSM 15574.

Corvus brachyrhynchos Brehn 1822
Common Crow

MATERIAL: Coracoid; humeri (2); ulnae (2); tibiotarsus; tarsometatarsi (3). UF/FSM 22538–22546.

DISCUSSION

McCoy (1963) identified 392 avian fossils representing 52 species (with corrections to his identifications, 47) from the Itchtucknee River deposits. The 1362 specimens reported here represent 56 species. The total number of species (see Table 1) reported from the Itchtucknee River now stands at 67.

In his paper, McCoy (1963) described three new species: *Palaeophoyx columbiana, Anas itchtucknee,* and *Gallinula brodkorbi*. As mentioned earlier, *Palaeophoyx columbiana* is a synonym of *Botaurus lentiginosus*. *Gallinula brodkorbi,* although considered a temporal subspecies of *G. chloropus* by some (Olson 1977), is here considered a valid species. I have examined the type of *Anas itchtucknee,* but on the basis of the available comparative material, both fossil and Recent, I was not able to prove either that it was or was not a valid paleospecies. I did not find any additional specimens of anatids that could be referred to the species, and am inclined to doubt its validity. Late Pleistocene anatids are rather difficult to identify because of the close relationship of the living species to which we try to refer the fossils, and because of the large intraspecific size and osteological variation that occurs in that group. Large series of comparative material are required to screen out this variation, and such series are not always available.

There are only seven (excluding the unknown accipitrid) extinct species, or 10 percent of the total number, present in the avifauna, and they represent only 3 percent of the specimens and 4 percent of the individuals recorded. If *Gallinula brodkorbi* is excluded, the six remaining extinct species represent only one percent of the specimens and three percent of the individuals. Thus, the portion of the avifauna consisting of extinct species is very small. When one considers that one species, *Ectopistes migratorius,* was recently extirpated by man, that two may be direct ancestors of living forms (*Gymnogyps amplus—Gymnogyps californianus*; *Gallinula brodkorbi—Gallinula chloropus*), and that only one of the others (*Ciconia maltha*) is reasonably well known, it becomes apparent that we are dealing with essentially a modern avifauna. Three of the seven extinct species (*Ciconia maltha, Gymnogyps amplus,* and *Ectopistes migratorius*) are also known from the deposits at Rancho La Brea, California, for which the oldest available date is approximately 40,000 B.P. In view of all of the above, McCoy's (1963) suggestion of a mid-Wisconsinan age for the Itchtucknee River deposits seems quite reasonable, and if this date is in error I would suggest that it is too old.

From an analysis of the fossil material he studied, McCoy (1963) concluded that extensive freshwater pond and marshy conditions prevailed at the time of deposition of the fossils. The additional material reported here completely supports his conclusion. Of the 20 most abundant species, only two, *Meleagris gallopavo* and *Pandion haliaetus,* are not strictly pond or marsh dwellers, although even the latter feeds primarily in the water. Only 17 of the remaining 47 species known from the avifauna can be considered non-aquatic, and they, plus *M. gallopavo,* make up only 12 percent of the total number of specimens, or 13 percent of the minimum number of individuals. The 26 species, 39 percent of the total, of grebes and anatids alone account for 62 percent of the specimens, or 58 percent of the minimum number of individuals. The predominance of aquatic birds and the lack of any species in the avifauna that could be considered marine strongly indicates extensive freshwater pond and marsh conditions.

The significance of *Milvago readei* in the late Pleistocene of Florida, in addition to what it suggests about evolution and dispersal patterns within the genus, lies in the implication that many avian species of South or Central American origin accompanied the large mammals of similar origin into Florida via the Gulf Coast Savanna Corridor during glacial periods. It would appear more likely that suites of savanna-adapted birds rather than just one or two species moved into Florida during the periods of lesser rainfall and more open country than now, only to retreat or become extinct when the climate returned to more humid conditions and the open country disappeared during interglacial periods. We should, therefore, expect to find additional South American forms in glacial-age deposits of Florida. We must also bear in mind that Florida could have acted as a major dispersal route for avian species that populated the Antilles.

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A REVIEW OF THE OSTEOLOGY AND PALEONTOLOGY OF TURKEYS (AVES: MELEAGRIDINAE)

By David W. Steadman[1]

ABSTRACT: A study of the comparative osteology of specimens of all known species of living and extinct turkeys results in the recognition within the Meleagridinae of three genera: *Rhegminornis* Wetmore, *Proagriocharis* Martin and Tate, and *Meleagris* Linnaeus. *Meleagris* contains all diagnostic specimens of Blancan and younger ages, including both living species. The genera *Agriocharis* Chapman and *Parapavo* L. Miller are synonymized with *Meleagris,* and the species *Meleagris alta* Marsh and *Meleagris tridens* Wetmore are synonymized with *Meleagris gallopavo*. Evidence suggests that since at least Blancan times species in the lineage leading to *Meleagris gallopavo* have continuously occupied the southern United States. *Meleagris gallopavo* is absent from pre-Rancholabrean deposits.

Turkeys are large gallinaceous birds comprising the subfamily Meleagridinae of the family Phasianidae. All living and extinct species of this subfamily are known only from the New World. The fossil record of turkeys begins with *Rhegminornis calobates* Wetmore (1943) from the Lower Miocene (Hemingfordian) of Florida. This poorly known form has characters of both the Phasianinae and the Meleagridinae. A much larger unnamed species is represented by a single, rather undiagnostic, element from the Upper Miocene deposits in Virginia. The earliest certain turkey is *Proagriocharis kimballensis* Martin and Tate (1970) from the Upper Pliocene (Hemphillian) of Nebraska. Fossils of turkeys are relatively common in the Pleistocene, and several distinct species are recognized. Table 1 lists the fossil localities from which the specimens came that I examined in this study, while Figure 1 shows the geographical distributions of all species of extinct and living turkeys. The nomenclature used in Table 1, although based on evidence presented later in this paper, is given now to maintain consistency throughout the paper.

The stimulus of this review of the osteology and paleontology of turkeys was the discovery of large numbers of fossils from two Pleistocene sites in Florida: Inglis IA, of earliest Irvingtonian age; and Coleman IIA, late Irvingtonian in age. These specimens differed significantly from the living *Meleagris gallopavo* Linnaeus, and appeared to resemble several poorly known extinct forms previously unknown in eastern North America. The Inglis IA site, with approximately 1240 specimens representing a minimum of 44 individuals, and the Coleman IIA site, with approximately 320 elements representing a minimum of 17 individuals, provide the earliest adequate samples for an assessment of individual variation in fossil turkeys. These samples thus provide excellent standards for comparison with fossil turkeys from other localities that are typically more fragmentary and less numerous.

Prior to the Inglis and Coleman finds, large samples of fossil turkeys were known from only three species, all of Rancholabrean age. These species are *M. crassipes* L. Miller (1940), *M. californica* (L. Miller 1909), and *M. gallopavo*. The relationships between the later forms and the rarer, earlier species were poorly known. This paper compares all extinct and living species of turkeys, incorporating the large Irvingtonian samples in an effort to determine the relationships among the various meleagridines. A revised classification and possible phylogeny are proposed, based on these comparisons.

COMPARATIVE OSTEOLOGY

The study of fossil turkeys is complicated by their great sexual dimorphism, males being much larger than females. In the absence of qualitative osteological characters, a male of a small species might easily be confused with a female of a larger species. This problem is especially acute when a fossil site yields too few specimens to assess intraspecific size variation. This problem is largely alleviated, however, when enough fossils are recovered and two distinct size classes can be distinguished. This is the case at Inglis IA, Coleman IIA, Ichetucknee River, Rancho La Brea, and a few other sites. When specimens from a particular site are not qualitatively separable from two or more known species, the size of the fossils will determine the identification. This identification must be considered tentative because of the great intraspecific size variation. The large size differences found in turkey bones often make direct comparisons difficult, hence the extensive use of the term "relatively" in the following comparisons.

In undertaking the studies of comparative osteology, my original approach was to compare *Meleagris gallopavo* with *M.* (=*Agriocharis*) *ocellata* and *M.* (=*Parapavo*) *californica* and, by searching for generic characters, determine to which genus the Inglis IA and Coleman IIA specimens belonged. It soon became apparent, however, that diagnostic characters are few and quite subtle. A broader approach was then taken

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in which each form was closely examined without reference to its supposed generic status.

With the notable exception of the work of Howard (1927), most characters of the various reputed genera and species of fossil turkeys have been based on only one or two individual specimens and do not hold when larger series of fossils or comparative material are examined. My findings often contradict previously published descriptions, the discrepancies being due largely, I believe, to the use of inadequate series of modern skeletons by earlier workers. The comparisons below are based on (1) the complete skeletons of 16 individuals of *Meleagris gallopavo* (8♂, 8♀) and 7 of *M. ocellata* (3♂, 4♀); (2) two partial tarsometatarsi of *Rhegminornis calobates*; (3) the holotype coracoid and three partial tarsometatarsi of *Proagriocharis kimballensis*; (4) all of the material of *M. progenes* reported by Brodkorb (1964b); (5) the paratype tarsometatarsus of *M. leopoldi*; (6) a cast of the holotype humerus of *M. anza*; (7) all of the Inglis IA and Coleman IIA specimens; (8) one to nine specimens of each element of *M. californica* from Rancho La Brea; and (9) one to eight specimens of each known element of *M. crassipes* from San Josecito Cave. These statements in turn form the basis for comparing specimens from all other sites.

The comparative osteological data presented below are roughly quantified in Tables 2 and 3. These tables will be discussed more fully in the Systematics section. Figures 2 through 7, based on a specimen of *M. gallopavo osceola*, explain the various measurements of Tables 4 through 22. In Tables 4 through 22, an asterisk (*) follows a measurement taken from a slightly damaged specimen. The actual value of the measurements would range from 1 to 5 percent greater than the reported value if the specimens were not damaged. Measurements followed by two asterisks (**) were taken from more severly damaged specimens in which the actual value would range from 5 to 10 percent greater than the reported value. Means that include one or more of these measurements are also followed by an asterisk. Measurements followed by "A" are careful approximations of the actual value.

CRANIUM

Howard 1927: Pls. 1, 2.

1. The interfrontal depression (Howard 1927: Pl. 1, Fig. 4e) is usually shallower in *M. ocellata* than in Inglis and Coleman specimens, *M. californica,* or *M. gallopavo.* This contradicts Howard (1927), who reported a greater depression in *M. californica* than in *M. gallopavo,* and a variable depth in *M. ocellata.*

2. The supraorbital processes of the frontals in ventral view are even with or lateral to the postorbital process in *M. ocellata*; in other forms they do not extend to the postorbital process. Inglis specimens are damaged in this area. This contradicts Howard (1927), who reported a similar amount of flaring of the supraorbital process in *M. californica* as in *M. ocellata,* with a lesser amount in *M. gallopavo.*

3. The amount of tapering as the frontals approach parietals in dorsal view (Howard 1927: Pl. 1, Figs. 1–4) is usually greater in *M. ocellata* than in Coleman fossils or *M. gallopavo*; in Inglis fossils and *M. californica* it may resemble any of the above forms. Howard (1927) also noted more tapering in *M. ocellata* than in *M. gallopavo,* with *M. californica* being intermediate.

4. The frontals in lateral view are usually more protrudent above the parietals (Howard 1927: Pl. 2, Fig. 1d), resulting in a larger depression along the fronto-parietal suture, in *M. californica* and *M. gallopavo* than in Coleman specimens or *M. ocellata.* Inglis specimens may resemble any of the above. This contradicts Howard (1927), who noted the lack of a fronto-parietal depression in *M. gallopavo* and its presence in *M. californica* and *M. ocellata,* while reporting a higher relative parietal height (i.e., a lower relative frontal height) in *M. gallopavo* than in *M. ocellata,* both of which were said to be higher than in *M. californica.*

5. The foramen magnum is circular to oblong to triangular in *M. ocellata,* circular to oblong in *M. gallopavo,* and circular in Coleman and Inglis fossils and *M. californica.*

Howard (1927) found the cranium of *M. californica* to be more similar to that of *M. ocellata* than to that of *M. gallopavo,* while I find that *M. californica, M. gallopavo,* and *M. ocellata* are not consistently separable from each other by any cranial characters. Inglis and Coleman specimens closely resemble these three species, which are certainly not generically distinct on the basis of their crania.

PREMAXILLA

Howard 1927: Pl. 1.

1. The portion of the premaxilla anterior to the nares is usually narrower relative to its length in *M. gallopavo* than in *M. ocellata* or *M. californica. M. progenes* and Inglis specimens are damaged in this area. Howard (1928) and Brodkorb (1964b) found no individuals in which this character does not hold.

2. The premaxilla is relatively deeper in *M. gallopavo* than in other forms, as noted by Howard (1928) and Brodkorb (1964b).

3. Two ventral foramina immediately anterior to the choanae are present in *M. progenes* but are absent in other turkeys (Brodkorb 1964b). These are not to be confused with the pair (rarely more) of foramina located nearer to the anterior end than to the choanae, which may occur in any of the forms.

M. progenes is distinct from all other forms in character 3. Inglis fossils, *M. ocellata* and *M. californica,* are more similar to each other than to *M. gallopavo* in other characters of the premaxilla. Howard (1928) noted the greater resemblance of *M. californica* to *M. ocellata* than to *M. gallopavo.* However, none of the differences seen in the premaxilla of turkeys appear to be of generic value, particularly in view of the apparent evolutionary plasticity of bill morphology in certain birds.

MANDIBLE

1. The postarticular process is more expanded dorsoventrally, usually longer, and usually more laterally compressed in *M. ocellata* than in *M. gallopavo.* All fossil specimens examined are damaged in this area.

2. The rami are usually relatively larger in *M. ocellata* than in *M. gallopavo.* All fossil specimens examined are damaged in this area.

3. The mandibular foramen is usually relatively larger in *M. ocellata* than in *M. gallopavo.* All fossil specimens examined are damaged in this area.

4. The dentary at the mandibular symphysis is slightly narrower and usually slightly longer in *M. gallopavo* than in *M. ocellata.* The other forms are similar to *M. ocellata* in width,

but are shorter at the symphysis than either *M. ocellata* or *M. gallopavo*. Brodkorb (1964b) reported a narrower and longer dentary in *M. gallopavo* than in *M. progenes* or *M. ocellata*, but noted no variation in this character.

The mandible of *M. gallopavo* is usually distinct from that of *M. ocellata*. Fossil forms resemble *M. ocellata* more than *M. gallopavo*, but this is based only on character 4.

STERNUM

Howard 1927: Pls. 3, 4.

1. The manubrium is directed more dorsad in *M. gallopavo* than in other forms.

2. The manubrium in dorsal view is roughly triangular in shape in all turkeys, the sides of the triangle being more interrupted by a projection of the dorsal lip of the coracoidal sulcus in some Coleman specimens and in all *M. ocellata* than in other forms. This finding is consistent with that of Howard (1927, 1963), who found the shape of the manubrium in *M. californica* to be closer to that in *M. gallopavo* than in *M. ocellata*. However, I see no consistent difference in the width of any portion of the triangular area, which was reported by Howard (1963) to be wider in *M. gallopavo* and *M. ocellata* than in the Vallecito Creek specimen or *M. californica*.

3. The dorsal manubrial spine in lateral view is deeper in some *M. californica* and in all *M. gallopavo* than in Inglis or Coleman specimens or *M. ocellata*, in agreement with Howard (1963), who also found this projection to be shallower in the Vallecito Creek specimen than in *M. gallopavo*.

4. The ventral manubrial spine in lateral view is more rounded in *M. ocellata* than in *M. gallopavo*, in which it is pointed or squared. All fossils examined are damaged in this area.

5. The coracoidal sulcus is relatively shallower in *M. ocellata* than in *M. californica* or *M. gallopavo*, largely because of the lesser development of the ventral lip. Inglis specimens are usually similar to *M. ocellata*, while Coleman specimens are usually similar to *M. californica* or *M. gallopavo*.

6. The dorsal surface is usually more pneumatic in Inglis and Coleman specimens than in *M. californica*, *M. gallopavo*, or *M. ocellata*.

The sternum in *M. californica* resembles that of *M. gallopavo* more than that of *M. ocellata*, while Inglis and Coleman specimens resemble that of *M. ocellata* or *M. californica* more than that of *M. gallopavo*.

FURCULA

Fig. 8; Howard 1927: Pl. 5.

1. The rami in dorsal view are usually straighter in *M. gallopavo* than in *M. ocellata*. All fossils examined are damaged in this area. Howard (1927:5) found the rami to be "straight-sided" in *M. californica* and *M. gallopavo* and "curved outward" in *M. ocellata*, but she noted no variation in this character.

2. The dorsal surfaces of the rami in lateral view are slightly concave in *M. ocellata*; in *M. gallopavo* they may be straight, slightly concave, slightly convex, or sigmoid (slightly convex on the sternal end and slightly concave on the scapular end). All fossils examined are damaged in this area.

3. The rami are stoutest in Inglis fossils and narrowest in *M. gallopavo*, with *M. californica* and *M. ocellata* being intermediate.

4. The rami near the symphysis are much more strongly flattened dorsoventrally, especially on the internal side, in *M. gallopavo* than in Inglis specimens or *M. californica*, with *M. ocellata* being intermediate.

5. The intermuscular lines convergent on the dorsal surface of the symphysis are much more distinct in Inglis specimens than in the other forms.

6. The intermuscular lines convergent on the ventral surface of the symphysis are usually more distinct in Inglis specimens and *M. californica* than in *M. gallopavo* or *M. ocellata*. This agrees with the findings of Howard (1927).

7. The hypocleidium is usually relatively shorter in *M. ocellata* than in *M. californica* or *M. gallopavo*. Inglis specimens are damaged in area.

8. The hypocleidium is much more expanded dorsoventrally in Inglis specimens than in *M. gallopavo* or *M. ocellata*, with *M. californica* being intermediate.

Howard (1927) regarded *M. californica* as generically distinct from *M. gallopavo* and *M. ocellata* on the basis of furcular characters, most of which are now seen to be only average differences. In characters 3, 5, and 8, the Inglis specimens differ from turkeys and resemble all species of Phasianinae examined.

CORACOID

Howard 1927: Pls. 6, 7.

1. The sternal facet is deeper internally and more tapered externally in most Coleman specimens, most *M. californica*, and in *M. ocellata* than in *Proagriocharis kimballensis*, Inglis specimens, or *M. gallopavo*. It is deep internally, but only slightly tapered externally, in *M. crassipes*. The specimen of *M. progenes* is damaged in this area.

2. The pneumatic foramen is extremely variable in relative size in all forms. Martin and Tate (1970:215) used the small pneumatic "fossa" (foramen?) of *P. kimballensis* to separate it from other turkeys, but all other forms may have an equally small pneumatic foramen.

3. The inner dorsal intermuscular line is curved farther away from the inner edge of the shaft in *P. kimballensis* than in other turkeys, as stated by Martin and Tate (1970). Howard (1927) correctly reported a similar amount of curvature in *M. gallopavo* and *M. californica*, but regarded this as being greater than in *M. ocellata*. Brodkorb (1964b) found this line to be curved farther away in *M. gallopavo* and *M. californica* than in *M. ocellata*, with *M. progenes* being intermediate. However, the individuals of each of these four species that I examined had a similar amount of curvature.

4. The inner dorsal intermuscular line is longer, extending to the sternal facet, in *M. crassipes* than in other forms, among which this line usually extends farther sternally in Inglis specimens. The specimens of *P. kimballensis* and *M. progenes* are damaged in this area.

5. The outer dorsal intermuscular line curves away from the outer edge of the shaft more in *M. progenes*, *M. crassipes*, and some *M. ocellata* than in other forms, contradicting Brodkorb (1964b), and Martin and Tate (1970), who reported more curvature in *M. progenes* and in *Proagriocharis*, respectively, than in other species.

6. The procoracoid may be of similar shape and extent in

all forms, contradicting Martin and Tate (1970), who found a more blunt procoracoid in *P. kimballensis* and *M. californica* than in *M. ocellata* or *M. gallopavo*.

7. The scapular facet is more rounded in *P. kimballensis*, some Inglis fossils, some *M. californica*, and some *M. crassipes* than in other turkeys, generally agreeing with Howard (1927) and Martin and Tate (1970).

8. The triosseal canal is deeper, producing a thinner neck, in *P. kimballensis* than in other turkeys, as stated by Martin and Tate (1970).

9. The humeral end in dorsal view may be inflected from the axis of the shaft similarly in all forms, contradicting Brodkorb (1964b), who reported more inflection in *M. progenes* than in *M. gallopavo* or *M. ocellata*.

10. The furcular facet is less protrudent from the neck (joining it more smoothly) in a few Coleman fossils, all *M. californica*, most *M. gallopavo*, and a few *M. ocellata* than in other forms. This contradicts Brodkorb (1964b), who found no overlap between *M. gallopavo* and *M. ocellata*, and Martin and Tate (1970:214–215), who stated that *P. kimballensis* "resembles *Agriocharis* [*ocellata*] and differs from *Parapavo* [*californicus*] and *Meleagris* [*gallopavo*] in that the head is raised above the inner surface of the neck."

11. The furcular facet is notched in *P. kimballensis* and in Inglis and Coleman specimens, unnotched in *M. progenes*, and variable in all other forms. Howard (1927:6) overlooked this variability in reporting a "slight notch" in *M. californica*, which she considered to be most similar to *M. gallopavo*, and a "shallow notch farther removed from the interior border" in *M. ocellata*. Martin and Tate (1970:214) also found no variability and reported an "indistinct mid-ventral notch" in *P. kimballensis* and *M. californica* and the absence of the same in *M. gallopavo* and *M. ocellata*.

12. The furcular facet in medial view is shallower relative to the depth of the shaft in *M. crassipes* than in other forms. However, no consistent difference in its overall shape was noted, thus contradicting Howard (1927), who found it to be oval in outline in *M. gallopavo* and *M. californica*, and more rounded in *M. ocellata*.

13. The attachment of Lig. humero-coracoideum anterius inferior ("coracohumeral ligament") may be similarly shaped in all turkeys, contradicting Martin and Tate (1970), who found it to be elongate in *P. kimballensis*, but triangular in other turkeys.

14. The attachment of Lig. humero-coracoideum anterius inferior has a distinct external border in all turkeys as stated by Howard (1927). Martin and Tate (1970) found it to be indistinct in *P. kimballensis*, but breakage obscures this character.

15. The external border of the attachment of Lig. humero-coracoideum anterius inferior reveals no consistent differences in any turkeys, contradicting Howard (1927), who found it to be more abrupt in *M. gallopavo* than in *M. ocellata*, with *M. californica* being intermediate.

16. The head is quite variable in shape in all forms, among which no consistent differences were found, thus disagreeing with Martin and Tate (1970), who reported the head to be oval in *P. kimballensis* and *M. californica* and not oval in *M. gallopavo* and *M. ocellata*.

17. The head in internal view is connected to the neck for a lesser distance in *P. kimballensis* than in *M. progenes*, *M. californica*, *M. gallopavo*, or *M. ocellata*. *Meleagris crassipes* is intermediate. This contradicts Brodkorb (1964b), who found the head to have a less extensive connection to the neck, i.e., to be more "free" (Brodkorb 1964b) from the neck, in *M. progenes* and *M. ocellata* than in *M. gallopavo*. Inglis and Coleman fossils may be similar to any of the above forms, thus contradicting Martin and Tate (1970), who found the head connected to the neck less in *P. kimballensis* than in any other turkey.

Martin and Tate (1970) regarded the coracoid of *P. kimballensis* to be most similar to that of *M. ocellata*, with some resemblances to *M. californica*. They did not compare it qualitatively with *M. progenes*. The coracoid of *P. kimballensis* is most similar to that of the Inglis species and least similar to that of *M. progenes* and *M. californica*. The perceived lack of similarity between *P. kimballensis* and *M. progenes* may be at least partly due to the presence of only one fairly complete coracoid for each.

Brodkorb (1964b) found the coracoid of *M. progenes* to resemble that of *M. ocellata* more than that of *M. gallopavo*, while I find that *M. progenes* does not resemble either living species more than the other.

Coracoids of *M. gallopavo*, *M. ocellata*, and the Coleman species are very similar to each other. As with other elements, Inglis and Coleman specimens are closer to each other than to any other forms.

Howard (1927) considered the coracoid of *M. californica* generically separable from that of *M. gallopavo* and *M. ocellata*, with a closer resemblance to *M. gallopavo*. However, *M. californica* does not consistently differ from *M. gallopavo* or *M. ocellata* in any of the 15 characters listed.

SCAPULA

Fig. 9; Howard 1927: Pls. 7, 8.

1. The acromion is usually less pointed in Coleman specimens and *M. gallopavo* than in Inglis specimens, *M. ocellata*, or *M. californica*. The specimens of *M. progenes* are damaged in this area.

2. The furcular articulation in proximal view is usually deeper relative to the depth of the glenoid facet in *M. californica* and *M. ocellata* than in *M. progenes*, Inglis and Coleman specimens, or *M. gallopavo*, thus agreeing with Howard (1927).

3. The base of the shaft in dorsal view lacks a pneumatic foramen in *M. progenes* and in Inglis fossils, while Coleman fossils, *M. californica*, *M. gallopavo*, and *M. ocellata* have a pneumatic foramen of variable size. Wetmore (1944:98) reported a non-pneumatic scapula from Rexroad as "Meleagrididae sp.?". Brodkorb (1964b) tentatively referred two similar scapulae from Rexroad to *M. progenes*. Both authors noted that the Rexroad specimens differed from other known species of turkeys in this character.

The structure of the scapula is very similar in all forms that have a pneumatic foramen. In agreement with Howard (1927), I tentatively regard *M. californica* as being more similar to *M. ocellata* than to *M. gallopavo* in its scapular structure. Evolutionary implications of a foraminate versus non-foraminate scapula are discussed below in the section on evolution.

HUMERUS

Howard 1927: Pl. 2.

1. The head is similar in relative size in all forms, contradicting Howard (1927), who reported a more pronounced head in *M. californica* than in either living species.

2. The external tuberosity in males is usually less prominent in Inglis specimens and *M. crassipes* than in other forms. No differences were seen among females.

3. The head protrudes more anconally above the attachment of the deltoid muscle in *M. gallopavo* than in most Inglis or Coleman specimens, most *M. californica,* most *M. crassipes,* or most *M. ocellata,* partially contradicting Howard (1927), who reported greater protrusion in *M. gallopavo* than in *M. ocellata,* with *M. californica* being intermediate. The Vallecito Creek specimen is damaged in this area. Cracraft (1968) noted the variability of this character.

4. The capital groove is usually shallower and narrower in *M. ocellata* than in *M. gallopavo.* Other forms are similar to one or the other of the above species. The Vallecito Creek specimen is damaged in this area.

5. The medial rim of the pneumatic foramen has less proximal extension and is less clearly defined in some Coleman specimens and in all *M. ocellata* than in other forms.

6. The deltoid crest in lateral view usually has a more pointed apex in Inglis specimens and *M. ocellata* than in Coleman specimens, *M. californica, M. gallopavo* or *M. crassipes.* The Vallecito Creek specimen is damaged in this area.

7. The scar of M. latissimus dorsi is deeply depressed, especially its distal portion, in the Vallecito Creek specimen, usually in *M. gallopavo,* rarely in Inglis and Coleman specimens, *M. californica* and *M. ocellata,* and never in *M. crassipes.* It is never quite as deep in *M. ocellata* as in the Vallecito Creek specimen. This contradicts Howard (1927:8), who found it to be deep in *M. gallopavo* and shallow in *M. ocellata,* with *M. californica* resembling either species. She added, "A certain variability may be noted in the *Meleagris* [*gallopavo*] specimens and might be found in *Agriocharis* [*ocellata*] as well, were more material available." Howard (1963) found this muscle scar to be deep in the Vallecito Creek turkey, but did not consider it in determining the relationship of the fossil.

8. The shaft of the Vallecito Creek specimen in palmar or anconal view is more decurved than in other forms. However, this is probably an artifact of preparation, the specimen being broken into two pieces and glued together immediately distal to the scar of M. latissimus dorsi.

9. The brachial depression is deeper in the Vallecito Creek specimen than in other forms, possibly because of crushing, as stated by Howard (1963). It is nearly as deep in some Inglis and Coleman specimens and some *M. crassipes* as in the Vallecito Creek specimen.

10. The attachment of M. pronator brevis faces more palmad and less mediad in the Vallecito Creek specimen, most Inglis and Coleman specimens, and most *M. ocellata* than in *M. californica,* most *M. crassipes,* or most *M. gallopavo.* Howard (1963) noted no variation in reporting it to face more palmad in the Vallecito Creek specimen and *M. ocellata* than in *M. gallopavo.*

11. The prominence proximal to the attachment of the anterior articular ligament is usually sharper and more protrudent in Coleman and Inglis specimens than in other forms.

12. The attachment of the anterior articular ligament faces more laterad in the Vallecito Creek specimen (Howard 1963) and some Inglis specimens than in other forms.

13. The external condyle usually has a more pointed proximal end, especially in males, in Coleman specimens and *M. gallopavo* than in Inglis specimens, *M. crassipes,* or *M. ocellata;* and *M. californica* may be similar to any of the above forms. Although it is rounded in the Vallecito Creek specimen, it resembles certain individuals of all other forms, thus contradicting Howard (1963), who stated it to be more rounded in the Vallecito Creek specimen and *M. ocellata* than in *M. gallopavo* or *M. californica.*

14. The external condyle has the greatest medial curvature in those specimens with the most pointed external condyles (see character 13) and vice versa. This varies exactly as character 13.

The status of the Vallecito Creek specimen in characters 7, 8, and 9 is probably a result of its poor preservation, and these characters are, therefore, not included in Table 2. See page 143 for a further discussion of the Vallecito Creek humerus.

With the exception of the Vallecito Creek specimen, the least similarity in the humerus is seen between *M. gallopavo* and specimens from Inglis, and between *M. gallopavo* and *M. ocellata.* The most similarity is between *M. californica* and *M. crassipes.* Only in character 5, in which *M. ocellata* differs from all forms except some Coleman specimens, is an absolute distinction seen between any two forms represented by more than one specimen.

ULNA

Howard 1927: Pls. 1, 8.

1. The shaft in lateral view in males is more curved in *M. crassipes* and *M. ocellata* than in *M. californica* or *M. gallopavo.* Males from Inglis and Coleman may resemble any of the above forms. No difference is seen between females of any forms. Curvature of the shaft generally increases as ulnar size decreases.

2. Howard (1927) reported a more marked distal overhang and a narrower distal border in the external cotyla in *M. gallopavo* than in *M. ocellata* or *M. californica,* but this is not apparent to me.

I detected no other valid characters in the ulna, which appears to be the least diagnostic major limb bone in turkeys.

RADIUS

Howard 1927: Pl. 7.

1. The lateral ridge in the distal portion of the shaft is usually less distinct in *M. ocellata* than in other forms. Howard (1927) noted several differences in the shape and position of this ridge in *M. californica, M. ocellata,* and *M. gallopavo,* but these differences are not apparent to me.

2. The distal ligamental prominence is usually less protrudent mediad in *M. ocellata* than in other forms.

3. The distal tendinal groove is usually deeper, especially in its distal portion, and of greater proximal extent, in *M. ocellata* than in other forms. The condition in *M. ocellata* is similar to that stated by Howard (1927). However, she found this groove to be only a faint notch in *M. californica,* while being broad and shallow in *M. gallopavo,* characters which I find to be inconsistent.

Howard (1927) found the radius of *M. californica* to resemble that of *M. ocellata* more than that of *M. gallopavo,* but my data show that *M. californica* resembles *M. gallopavo* more than *M. ocellata* in this element. In fact, the radii from Inglis and Coleman and those of *M. californica, M. crassipes,* and *M. gallopavo* are alike in all three characters, and three average differences from all other known forms are seen in the radii of *M. ocellata.*

ULNARE

1. The ulnar base is wider relative to its length in Inglis fossils and *M. ocellata* than in *M. progenes* or *M. gallopavo,* contradicting Brodkorb (1964b), who found it relatively wider in *M. progenes* and *M. ocellata* than in *M. gallopavo.*

2. The ulnar base is not consistently different in height, contradicting Brodkorb (1964b), who found it high in *M. progenes* and *M. ocellata* and low in *M. gallopavo.*

CARPOMETACARPUS

Howard 1927: Pl. 9.

1. The inner trochlea is usually less notched in the proximal edge by Lig. internum ossi carpi ulnaris et metacarpi in *M. progenes* and *M. ocellata* than in other forms, contradicting Brodkorb (1964b), who reported a deeper notch in *M. progenes* and *M. gallopavo* than in *M. ocellata.*

2. The interior carpal fossa does not consistently differ in depth in any form, but the posterior carpal fossa is usually shallower in *M. ocellata* than in other forms, contradicting Brodkorb (1964b), who found both carpal fossae to be shallower in *M. progenes* and *M. ocellata* than in *M. gallopavo.*

3. The intermetacarpal tubercle, which may be fused or unfused to metacarpal III in all forms, as noted by Howard (1927), does not consistently differ in position. Brodkorb (1964b) found it positioned more distally in *M. gallopavo* than in *M. progenes,* which is true for all but one individual of *M. gallopavo* which I examined.

4. The facet for digit III does not consistently differ in relative length, contradicting Brodkorb (1964b), who reported a longer facet in *M. progenes* than in living turkeys.

The carpometacarpus of *M. progenes* is very similar to those of Inglis and Coleman specimens. Brodkorb (1964b) found *M. progenes* to be more similar to *M. ocellata* than to *M. gallopavo* in most characters of the carpometacarpus. However, my qualitative data do not reveal a closer resemblance of *M. progenes* to either of the living species. *M. ocellata* has the most distinctive carpometacarpus. Howard (1927) found no basis for relationships in this element.

PELVIS AND SYNSACRUM

1. The median dorsal ridge is usually relatively wider in *M. ocellata* than in *M. gallopavo.* All fossils examined are damaged in this area.

2. The anterior portion of the ilium usually flares more laterad in *M. gallopavo* than in *M. ocellata.* All fossils examined are damaged in this area.

3. The antitrochanter usually has a more decurved ventral border in Inglis and Coleman specimens and *M. gallopavo* than in *M. californica* or *M. ocellata.*

4. The area between the antitrochanter and the obturator foramen is usually more pneumatic in Inglis specimens than in other forms.

5. The ischium is usually more inflected caudally, appearing larger in caudal view, in *M. gallopavo* than in *M. ocellata.* All fossils examined are damaged in this area.

No absolute distinction is ever seen between *M. gallopavo* and *M. ocellata,* all characters being based upon average differences. Little can be said of fossil forms because of their poor condition.

FEMUR

Howard 1927: Pl. 9.

1. The lesser trochanter is notched by the groove for Lig. capsularis femoris to a variable depth in all forms, contradicting Howard (1927), who found it less distinctly grooved in *M. ocellata* than in *M. californica* or *M. gallopavo.* The single specimen of *M. progenes* is similar to individuals of all other forms, contradicting Brodkorb (1964b), who reported a more strongly notched lesser trochanter in *M. californica* and *M. gallopavo* than in *M. progenes* or *M. ocellata.*

2. The groove for Lig. capsularis femoris on the lateral surface of the shaft does not consistently differ in depth in any form, contradicting Brodkorb (1964b), who stated it to be deeper in *M. californica* and *M. gallopavo* than in *M. progenes* or *M. ocellata.*

3. The greater trochanter in medial view usually has a greater proximal extension in *M. gallopavo* than in *M. ocellata.* Inglis and Coleman fossils and *M. californica* may resemble any of the above forms. The specimens of *M. progenes* and *M. crassipes* are damaged in this area.

4. The shaft in medial view is usually less curved in *M. ocellata* than in other forms. The specimen of *M. progenes* is damaged in this area.

5. The posterior intermuscular lines may be fused or unfused in the middle portion of the shaft in all forms except possibly *M. progenes* (in the single known specimen of this species these lines are fused). Howard (1927) noted less convergence of these lines in *M. gallopavo* than in *M. ocellata* or *M. californica,* but Brodkorb (1964b:227) found these lines to be usually "fused along middle third of their length" in *M. ocellata* and *M. californica,* and "usually unfused, although the character is variable" in *M. gallopavo.*

6. The intercondylar groove is usually relatively deeper in *M. crassipes* than in other forms, all of which may resemble each other in depth. This contradicts Howard (1927), who found the intercondylar groove in *M. californica* to be broader but similar in depth to that in *M. gallopavo,* and deeper and narrower in *M. ocellata* than in either *M. californica* or *M. gallopavo.*

7. No other distinguishing characters are seen in the distal end. Howard (1927) noted a greater depth (relative to width) of the inner condyle in *M. californica* than in *M. gallopavo* or *M. ocellata,* and the latter two species were said to have an oblique angle at the junction of the posterior surface of the shaft and inner condyle, as opposed to nearly a right angle in *M. californica.* These characters are not apparent to me.

The three characters (1, 2, and 5) used by Brodkorb (1964b) in stating that *M. progenes* resembled *M. ocellata* more than *M. gallopavo* are found to vary in most species. Yet the femur of *M. progenes* still resembles that of *M. ocellata* or *M. californica* slightly more than that of *M. gallopavo*. Inglis and Coleman femora show perfect resemblance to each other, and both are also quite similar to that of *M. gallopavo, M. ocellata*, and *M. californica*. The femur of *M. ocellata* is least similar to that of *M. gallopavo* or *M. californica*.

TIBIOTARSUS

Howard 1927: Pls. 10, 11.

1. The inner cnemial crest is usually less protrudent laterally in *M. ocellata* than in Coleman specimens or *M. gallopavo*, and Inglis specimens and *M. californica* may resemble any of the above forms. *Meleagris progenes* and *M. crassipes* are damaged in this area. This finding contradicts that of Howard (1927:18), who reported this crest as "Most abruptly thrust toward outside in *Agriocharis* [*ocellata*]; *Parapavo* [*californicus*] similar to *Meleagris* [*gallopavo*] and *Pavo*." She said that her statement on *M. ocellata* agreed with that of L. Miller (1916a), who did not include *M. gallopavo* in his comparison. However, L. Miller did not say whether he was referring to the inner or to the outer cnemial crest. (One must read L. Miller (1916a) with caution because he used "*Agriocharis*" and "*Meleagris ocellatus*" interchangeably. When he spoke of "*Meleagris*," he seemed to be referring either to both *M. ocellata* and *M. gallopavo*, or only to *M. ocellata*.)

2. The internal ligamental prominence is larger in the only undamaged specimen of *M. progenes* than in most Inglis and Coleman specimens and all examples of other forms.

3. No other diagnostic characters are seen in the distal end. L. Miller (1916a) reported the condyles to be closer together and the tunnel under the supratendinal bridge to be larger in *M. ocellata* than in *M. californica*, but these differences are not apparent to me. Based on characters of the tibiotarsus, the affinities of *M. californica* to *M. ocellata* or *M. gallopavo* were unclear to Howard (1927). I agree with Howard and stress the similarity of the tibiotarsi of all turkeys. This statement is not without precedent, as A. Miller and Bowman (1956) and Brodkorb (1964b) have noted the lack of useful taxonomic characters in the distal end of the tibiotarsus in turkeys.

FIBULA

The lateral surface of the fibula in all turkeys is convex to some extent, but it is more convex in *M. californica* than in most Inglis specimens, all Coleman specimens, most *M. gallopavo*, and all *M. ocellata*, partially contradicting Howard (1927), who found it to be convex in *M. californica*, straight in *M. gallopavo*, and slightly convex in *M. ocellata*. Howard also noted variability in the fibula of *M. ocellata*, and regarded the fibula as being of little taxonomic value.

TARSOMETATARSUS

Figs. 10–14; Howard 1927: Pls. 12, 13.

The most diagnostic bone in turkeys is the tarsometatarsus, and many characters of this bone have been used to define various taxa of turkeys. Most important has been the bony spur core on the plantar side of the shaft, which in life is surrounded by a scutellum. Males have a spur, but it is normally absent in females. However, Williams and Austin (1969) estimated that more than 1 percent of the females of *M. gallopavo osceola* in their Florida study area had a spur on at least one leg. Pattee and Beasom (1977) also found at least one tarsal spur on 2 of 228 females of *M. gallopavo intermedia* in Texas.

The normal presence of rudimentary spurs in females of *M. ocellata* has often been cited as a significant difference between that species and *M. gallopavo*, and was used in the original generic diagnosis of *Agriocharis* (Chapman 1896). This rudiment is only a single dark, hardened, and slightly elevated scutellum that is located where the bony spur would be in a male. Its presence is not normally reflected in any way on the tarsometatarsal bone itself. Such a rudimentary spur is also present in females of *M. gallopavo* and is occasionally as developed as in *M. ocellata*.

The scutellum and inner bony spur core of males become increasingly pointed with age. Spur development in *M. gallopavo osceola* may begin at 6 months of age and is not completed by the end of the first year (Lovett Williams pers. comm.). Eaton and Moore (1965–66:39) found the spur core of *M. gallopavo silvestris* to be "only a knob" at age 9–10 months, "more prominent . . . well formed" at age 20–22 months, and "slightly more massive [than at age 20–22 months]" at age 29–33 months. I have noted that males of wild *M. ocellata* have a small (length, 8 to 15 mm), slightly pointed spur by age 8–9 months and develop long, sharply pointed spurs by age 2–3 years. However, the size and pointedness of the spur core seem to show no relationship to the total size of the bone. Eaton and Moore (1965–66:36), in reference to wild *M. gallopavo silvestris*, state, "The hind appendage [=leg], though reaching almost full length at 5–6 months continued to become more massive and developed the bony core for the spur between the tenth and twentieth months." Both the shortest and the longest of ten tarsometatarsi of males of *M. gallopavo osceola* that I measured had short, blunted spur cores. L. Miller (1916a) reported the weakest spur in the longest, and the strongest spur in the shortest, of 25 specimens of *M. californica* he examined.

I also examined the tarsometatarsi of the following species of Galliformes from the collection of Pierce Brodkorb, in addition to those of turkeys, to determine the relationships of *Rhegminornis calobates*: Odontophorinae—*Dendrortyx macroura, Callipepla squamata, Colinus virginianus*; Phasianinae—*Alectoris graeca, Francolinus sephaena, Pternistes swainsonii, Coturnix delegorguei, Caloperdix oculea, Gallus gallus, Crossoptilon auritum, Catreus wallichii, Syrmaticus ellioti, Chrysolophus pictus, Pavo muticus*; and Numididae—*Acryllium vulturinum*.

1. The small calcaneal ridge between the inner and outer calcaneal ridges is not consistently different in size in any form and may be absent in *M. gallopavo*. The specimens of *Rhegminornis calobates* and *M. progenes* are damaged in this area. My findings contradict those of L. Miller (1916a:91), who noted the well marked presence of this medial calcaneal ridge in *M. californica*, but found it to be "almost entirely wanting even in old specimens of *Meleagris gallopavo* . . . but faintly indicated in *M. ocellatus*." Although Wetmore (1924) also used this character, he noted its variability in *M. gallopavo* and commented on its decreased taxonomic significance. Howard (1927) found this ridge to be well developed in *M. ocellata* and *M. californica*, but 18 of her specimens of *M. gallopavo* lacked the ridge, and its development and position in the remaining

13 was variable. A. Miller and Bowman (1956) correctly stated that this ridge is not useful in separating *Meleagris* from *Parapavo*.

2. The large outer calcaneal ridge usually has less plantar protrusion in *M. ocellata* than in other forms, partially contradicting L. Miller (1916a), who reported it to be more prominent in *M. californica* than in *M. gallopavo* or *M. ocellata*. The specimens of *R. calobates* and *M. progenes* are damaged in this area.

3. The larger outer calcaneal ridge usually is relatively longer in *M. crassipes* than in *M. leopoldi*, Inglis and Coleman fossils, *M. gallopavo* or *M. ocellata*. It is either intermediate in length or similar to the shorter specimens of the forms above in *P. kimballensis* and *M. californica*. The specimens of *R. calobates* and *M. progenes* are damaged in this area. This contradicts L. Miller (1916a), who found it to be shorter in *M. gallopavo* and *M. ocellata* than in *M. californica*.

4. The internal cotyla protrudes more abruptly mediad in *M. gallopavo* than in *R. calobates*, *P. kimballensis*, *M. leopoldi*, several Inglis and Coleman specimens, several *M. californica*, several *M. crassipes*, most *M. ocellata*, and all species of Numidinae, Phasianinae, and Odontophorinae examined. The specimens of *M. progenes* are damaged in this area. Wetmore (1924:9) may have been referring to this same character when he attributed a "proportionally broader and heavier" head of the tarsometatarsus to *M. gallopavo* as compared to *M. californica*.

5. The lateral prominence of the external cotyla is usually slightly less developed in *M. crassipes* than in other turkeys. The specimens of *R. calobates* and *M. progenes* are damaged in this area.

6. Two narrow ridges are present above the tubercle for tibialis anticus in *R. calobates*, *P. kimballensis*, and all nonmeleagridine phasianids examined, but are absent in all known post-Hemphillian turkeys. The specimens of *M. progenes* are damaged in this area.

7. The tubercle for tibialis anticus is narrower but more prominent in *R. calobates* than in other forms, as stated by Olson and Farrand (1974). It is also narrower and more prominent in *R. calobates* than in all other phasianids examined except *Francolinus sephaena* and *Gallus gallus*, in which it is more prominent but equally narrow. The specimens of *M. progenes* are damaged in this area.

8. The acrotarsial groove on the shaft is usually shallower in *M. californica* and *M. crassipes* than in *M. leopoldi*, Inglis and Coleman specimens, or *M. gallopavo*. It is similar in *R. calobates* to shallower individuals of the last three forms listed above, but is shallower than in *M. leopoldi*. It is usually deeper in *P. kimballensis* and *M. ocellata* than in *R. calobates*, *M. leopoldi*, *M. californica*, or *M. crassipes*. Its depth is also quite variable within other phasianid subfamilies studied. The specimens of *M. progenes* are damaged in this area. This partially contradicts Olson and Farrand (1974), who reported a shallower groove in *R. calobates* than in *M. gallopavo* or *M. ocellata*.

9. The thin ossified intertendinal septum that extends from the hypotarsus nearly to the facet for the hallux is absent in *R. calobates*, but is present in all other turkeys and many other phasianids, as stated by Olson and Farrand (1974). They noted the probable lack of taxonomic significance in this character. The specimens of *M. progenes* are damaged in this area. This septum, absent in young (but full-sized) specimens of fossil and living turkeys, was found by Eaton and Moore (1965–66) to develop at age 5–6 months in females and 9–10 months in males of *M. gallopavo silvestris*.

10. The spur core is strongly curved upward in *P. kimballensis*, Inglis specimens, and *M. ocellata*, slightly to strongly curved upward in Coleman specimens, and straight to slightly upcurved in *M. californica*, *M. gallopavo*, and *M. crassipes* (see Fig. 4). The specimens of *M. progenes* and *M. leopoldi* are damaged in this area. No spur core is present on the known specimens of *R. calobates*.

11. The surface of the spur core is of similar roughness in all forms, contradicting Howard (1927:24), who described the spur core of *M. gallopavo* as "roughly built" and that of *M. californica* and *M. ocellata* as "well formed." Developing spur cores have a very rough surface, which becomes smoother with age. Full-length, pointed spur cores are of the same approximate smoothness in all species. Thus the distinction noted by Howard was probably due to age differences in her specimens.

12. The facet for hallux does not consistently differ in position or shape in any turkeys, while in other phasianids it may resemble that of turkeys or be more rounded and deeper. This contradicts Brodkorb (1964b), who reported it as low in *M. progenes*, rather low in *M. ocellata*, and elevated in *M. gallopavo*.

13. The inner intertrochlear foramen is rarely absent only in Inglis and Coleman specimens, *M. californica*, *M. gallopavo*, and *M. ocellata*. It is always present in varying degrees of development in other turkey specimens. Note that the five variable forms are the only turkeys for which a large sample is available. Howard (1927) noted variation in the development of this foramen in *M. californica*, *M. gallopavo*, and *M. ocellata*; A. Miller and Bowman (1956) also noted the inconsistency of this character. Olson and Farrand (1974) noted its presence in *R. calobates* as a meleagridine character to distinguish it from the Phasianidae (*sensu stricto*). However, this foramen may be present in specimens of *Colinus virginianus*, *Alectoris graeca*, *Pternistes swainsonii*, *Coturnix delegorguei*, *Caloperdix oculea*, *Gallus gallus*, *Crossoptilon auritum*, *Chrysolophus pictus*, and *Pavo muticus*.

14. The inner intertrochlear foramen is located lower in one specimen of *R. calobates* (PB 8447) than in all other phasianids examined. Olson and Farrand (1974) stated that it is in the same location in the holotype of *R. calobates* (MCZ 2331) as in *M. gallopavo*.

15. The lateral distal foramen is usually relatively lower in Inglis and Coleman specimens than in other turkeys, including *R. calobates*. Brodkorb (1964b) reported it to be low in *M. progenes* and *M. ocellata*, slightly higher in *M. leopoldi*, and high in *M. gallopavo* and *M. californica*, but these differences are not apparent to me.

16. The lateral distal foramen in plantar view is usually relatively larger in *M. crassipes* and usually smaller in *M. ocellata* than in other turkeys, including *R. calobates*. Olson and Farrand (1974) also reported it to be smaller in *M. ocellata* than in *M. gallopavo*, but reported it to be relatively smaller in *R. calobates* than in *M. gallopavo*. This is not true in specimens that I have examined. They also reported it to be more elongate in meleagridines than in phasianids (*sensu stricto*). However, it may be as relatively large and elongate in *Gallus gallus*, *Crossoptilon auritum*, or *Chrysolophus pictus* as in turkeys.

17. The inner trochlea is usually relatively wider in *M. cras-*

sipes than in other turkeys. The specimens of *R. calobates* are damaged in this area, and that of *P. kimballensis* was not available for study. Brodkorb (1964b) found it to be narrower in *M. progenes* and *M. gallopavo* than in *M. leopoldi* or *M. ocellata*, but I found no consistent difference in this character in these four species.

18. The inner trochlea in plantar view is situated more medially in some *M. ocellata* and all non-meleagridine phasianids examined than in other turkeys, including *R. calobates*. The specimen of *P. kimballensis* was not available for study.

19. The inner trochlea is less elevated in *R. calobates*, *M. leopoldi*, and two specimens of *M. crassipes* than in all other turkeys or all other phasianids examined except *Alectoris graeca*. The specimen of *P. kimballensis* was not available for study, but, in Fig. 1E of Martin and Tate (1970), it appears to be more elevated than in the above forms. Olson and Farrand (1974) reported it to be more elevated in turkeys than in other phasianids (*sensu stricto*), but this is not apparent to me.

20. The inner trochlea is usually situated more on the plantar surface in females of *M. ocellata* than in other turkeys, including *R. calobates*. The specimen of *P. kimballensis* was not available for study. This character is variable among non-meleagridine phasianids examined.

21. The middle trochlea has a similar amount of acrostarsial rotation in certain specimens of each species of turkey, including *R. calobates*, and may resemble certain species of Numididae, Phasianinae, and Odontophorinae. The specimen of *P. kimballensis* was not available for study. This contradicts Olson and Farrand (1974), who found the middle trochlea to be rotated more acrotarsiad in *M. gallopavo* and *R. calobates* than in other Galliformes.

22. The ridge in the proximal portion of the medial plantar border of the middle trochlea is usually less conspicuous in *M. californica* and *M. crassipes* than in other turkeys, including *R. calobates*. Wetmore (1924) also distinguished *M. gallopavo* from *M. californica* on this basis, but noted no variation in this character.

23. The outer trochlea does not vary significantly in its extent of plantar rotation in any turkey. The specimens of *R. calobates* and *P. kimballensis* were not available for study. This contradicts Wetmore (1924), who observed that both lateral trochleae were rotated more plantad in *M. ocellata* than in *M. californica* or *M. gallopavo*.

24. The outer trochlea is usually less elevated in *M. crassipes* than in other turkeys. It is more elevated in *R. calobates* than in other turkeys, as stated by Olson and Farrand (1974), and is also more elevated in *R. calobates* than in all other phasianids examined. The specimens of *P. kimballensis* are damaged in this area.

25. The intertrochlear notches are usually relatively narrower in *M. ocellata* than in *R. calobates* (only inner notch present), *M. progenes*, *M. leopoldi*, Inglis specimens, or *M. crassipes*. Other turkeys may resemble any of the above forms, but are least similar to *M. ocellata*. The specimens of *P. kimballensis* are damaged in this area. The intertrochlear notches of all non-meleagridine phasianids examined are similar to those of certain turkeys. This contradicts Brodkorb (1964b) who reported them to be wider in *M. progenes* than in other turkeys, and also Olson and Farrand (1974), who noted less divergent trochleae in *R. calobates* and *M. ocellata* than in *M. gallopavo*.

Table 3 presents a quantitative compilation of the 18 characters of the tarsometatarsus in which a significant difference is seen between at least two forms listed above. *Rhegminornis calobates* shows the lowest overall similarity to other forms, and possesses two typically phasianine characters (characters 6, 7). It is more similar to that of *Proagriocharis kimballensis* or *M. leopoldi* than to all other forms, to which it is consistently the most dissimilar species. The tarsometatarsus of *P. kimballensis* is more similar to that of later forms than is the tarsometatarsus of *R. calobates*, although retaining phasianine character 6. It is least similar to those of *M. crassipes*, and its modest degree of resemblance to all other forms is greatest with *M. progenes* and *M. leopoldi*. *Meleagris progenes* is very similar to *M. leopoldi*, Inglis and Coleman specimens, *M. gallopavo*, and *M. californica*. *Meleagris leopoldi* is very similar only to *M. progenes*, but it is quite different from only *R. calobates* and *M. crassipes*. Inglis specimens are very similar to those of *M. progenes* and the Coleman specimens, and the latter are also very similar to *M. progenes* and *M. gallopavo*. *M. gallopavo* has a high degree of resemblance to *M. progenes*, Coleman specimens, and *M. californica*, with the last also closely resembling *M. progenes*.

High levels of similarity of the magnitude noted between the tarsometatarsi of *M. progenes*, *M. leopoldi*, Inglis and Coleman specimens, *M. gallopavo*, and *M. californica* are not noted in *M. ocellata* or *M. crassipes*. These two species are very unlike each other and display only a modest degree of similarity to all forms but *R. calobates*, with the exception that *M. crassipes* is fairly similar to *M. californica* and quite dissimilar to *P. kimballensis*.

Ratios of all of the measurements of every element of the various taxa were computed and compared. These data, available from the author on request, prove to be of limited taxonomic value with the exception of the data on the tarsometatarsi of males. To my surprise, the greatest difference among all of the taxa in these proportions is often between Recent specimens of *M. gallopavo silvestris* and *M. g. osceola*. Thus, considering this high variability within a living species, I regard the use of intra-elemental proportions in the definition of extinct genera and species as being generally of very limited value, except as discussed below.

The angle of the spur core (Table 20: K) and the relative height of the spur core (Table 22: F/A, G/A) have traditionally been very important in the definition of various taxa of turkeys. It may be seen from my data that the angle of the spur core is smallest in *P. kimballensis* and *M. crassipes*, although both species are represented by only one individual. Next appears the intermediate group of *M. progenes*, *M. leopoldi*, Inglis and Coleman specimens, and *M. californica*. A gradation is seen in the various large samples from Florida, with a steadily increasing angle through time from Inglis to Coleman to Ichetucknee to modern *M. g. osceola*. Note the large amount of overlap between adjacent samples through this progression. Also note the high degree of variability in this angle within any given large sample. These data suggest the use of great caution when making taxonomic conclusions based upon only minor differences.

L. Miller (1940) reported angles of 39 and 79 degrees, respectively, for *M. crassipes* and *M. californica*, while A. Miller and Bowman (1956) reported angles of 53.0 to 58.5 degrees for *M. leopoldi*, 62.0 degrees in *M. californica*, and 63.5 to 71.5 degrees in *M. gallopavo*. Brodkorb (1964b) reported angles of 60 to 80 degrees in *M. gallopavo* and *M. californica*, while

Martin and Tate (1970) reported angles of less than 60 degrees in *P. kimballensis* (39 degrees) and "*Agriocharis*," and angles greater than 60 degrees in *M. californica* or *M. gallopavo*. Brodkorb (1964b) appears to have placed too much weight on this angle when he said, "Both *A. leopoldi* (A.H. Miller and Bowman 1956) and *A. crassipes* (L. Miller 1940) have the spur core low on the shaft and at an angle of less than 60 degrees, characters that require their removal from the genus *Meleagris*, in which they were described." However, both *M. gallopavo* and *M. californica* may commonly have a spur core angle of under 60 degrees (Table 20). Also, *M. crassipes* has a greater average relative height of the spur core than all other species (Table 22: F/A, G/A), with *M. californica* and *M. gallopavo* intermediate between it and the forms with lower spur cores (*M. leopoldi*, Inglis and Coleman specimens). Thus, the height of the spur core, which is very different in *M. crassipes* than in *M. leopoldi*, cannot be used as a generic character to separate both *M. crassipes* and *M. leopoldi* from *M. gallopavo*. *Proagriocharis kimballensis* and *M. progenes* have spur core heights that resemble those of many other species, and large samples of these species are needed before anything definitive can be stated. Note the high variability of this character in Coleman specimens, *M. gallopavo*, and *M. californica*, demonstrating the variation that may occur in large samples. L. Miller (1916a) first used spur core height as a taxonomic character, reporting a height of 40 to 41 percent in *M. californica*. Howard (1927) reported a height of 39.2 to 46.9 percent in *M. gallopavo*, 41.3 to 49.7 percent in *M. californica*, and 40.0 percent in *M. ocellata*, her figures corresponding to F/A of Table 22; the figures of more recent authors pertain to G/A. Noting no variation, L. Miller (1940) reported heights of 45 percent in *M. crassipes*, 43 percent in *M. gallopavo*, 42 percent in *M. californica*, and 35 percent in *M. ocellata*. The height (39.8 percent) in *M. leopoldi* reported by A.H. Miller and Bowman (1956) is a composite based on measurements from two different specimens; the 36.3 percent reported herein is based solely upon the paratype tarsometatarsus. Other values of A. Miller and Bowman (1956) are 41.7 to 46.0 percent in *M. californica*, 41.2 to 43.4 percent in *M. gallopavo*, and 36.0 percent in *M. ocellata*. The relative spur core height in *M. progenes*, described as "situated low" in the Rexroad specimen by Brodkorb (1964b:225), can be computed only from the tentatively referred specimen from Benson, Arizona. The *absolute* height of the spur core (Table 20: F, G) of the Rexroad specimen of *M. progenes* is about at the minimum range of Inglis specimens. Martin and Tate (1970) listed a height of 36 percent in *M. ocellata* and 42 percent in *P. kimballensis*, saying that the latter just overlaps the lower range of *M. gallopavo* and *M. californica*. However, the figure of 42 percent is erroneous, for assuming that their figures for total length (98 mm) and spur core height (40 mm) are correct, the relative spur core height would be 40.8 percent. The relative stoutness of the spur core (Table 22: H/J) is greatest in *M. crassipes*, and averages smallest in *M. ocellata*.

DISCUSSION OF FOSSIL TURKEYS BY LOCALITY

MIOCENE (HEMINGFORDIAN)

THOMAS FARM, Gilchrist County, Florida, *Rhegminornis calobates*. Tarsometatarsus (MCZ 2331, PB 8447–8449)—Table 21, Fig. 14; Figs. 1–2 of Olson and Farrand (1974), in which PB 8448 is mislabelled PB 1776. This species, originally described by Wetmore (1943) in the Jacanidae (Charadriiformes), was removed from the Jacanidae and placed in the Meleagridinae by Olson and Farrand (1974). While agreeing that it is a member of the Phasianidae (*sensu lato*), I feel that the known specimens of *R. calobates* are insufficient to place it unequivocally in the Meleagridinae, although such a placement may very well be correct. The four meleagridine characters of *R. calobates* used by Olson and Farrand to exclude it from the Phasianidae (*sensu stricto*) may be found in certain species of Phasianidae (see characters 13, 16, 19, 21). Using living species to define the characters of meleagridine versus non-meleagridine phasianids, *R. calobates* has characters of both groups, suggesting that a redefinition of these subfamilies would be necessary if one were going to include *R. calobates* in one of them. Such a redefinition would be of limited value at present because of our fragmentary knowledge of *R. calobates*. Also, it would tend to mask the intermediate nature of the specimens, and, as more specimens of *R. calobates* and other Tertiary phasianids become available, such redefinitions would become increasingly difficult and meaningless. I have not attempted to place *R. calobates* in a modern subfamily because of the apparently mosaic nature of its tarsometatarsus and its lack of other known elements.

An indication of the degree of similarity between *R. calobates* and various turkeys can be seen in Table 3. It is most similar to *Proagriocharis kimballensis* and *Meleagris leopoldi*, although every form except *P. kimballensis* is less similar to *R. calobates* than any other form. This, as well as overall size, suggests that *R. calobates* could be an early form of turkey, possibly near the ancestry of *P. kimballensis*. However, this hypothesis is very tentative at present as it is based on but one element. It must be kept in mind that the amounts of similarity seen in any of the relatively poorly known forms in Tables 2 and 3 may be an artifact of small sample sizes.

EARLY LATE MIOCENE (CLARENDONIAN?)

WESTMORELAND STATE PARK, Westmoreland County, Virginia. Claremont Member of Eastover Formation (Blackwelder and Ward, unpubl.; *fide* Lauck Ward). Meleagridinae, cf. *Meleagris*. Tibiotarsus (USNM 237260)—Table 19. This specimen is a left tibiotarsus with only a very small section of the shaft missing. It is slightly eroded and possibly from a juvenile and could not be distinguished qualitatively from tibiotarsi of *M. gallopavo* or *M. ocellata*. However, as the tibiotarsus of turkeys is nearly lacking in diagnostic characters (see page 137), positive assignment to *Meleagris* is not justified. Most importantly, however, this specimen documents the occurrence of a fairly large turkey as early as the late Miocene. Lacking comparable elements, nothing can be said of the affinities of this specimen to *Rhegminornis calobates* or *Proagriocharis kimballensis*, both of which are much smaller.

I carefully compared this specimen with all other Tertiary specimens of turkeys, as well as with skeletons of several genera of the Cracidae, as this family of Galliformes is known to occur in Tertiary fossil localities in North America (Brodkorb 1964a). All specimens reported herein have phasianid characters and can be distinguished from specimens of the Cracidae.

LATE MIOCENE OR EARLY PLIOCENE (HEMPHILLIAN)

UNSM COLL. LOC. FT-40, Frontier County, Nebraska. *Proagriocharis kimballensis*. Coracoid (UNSM 20033)—Table 4. Tarsometatarsus (UNSM 20035–20037)—Tables 20–22, Fig. 14; Fig. 1 (reduced by the printer beyond the authors' wishes) of Martin and Tate (1970). Described as a new genus and species by Martin and Tate (1970), I tentatively regard *P. kimballensis* as distinct from *Meleagris,* cautiously noting that this conclusion is based upon only two elements of the skeleton. Fortunately, both spurred and unspurred tarsometatarsi exist of *P. kimballensis,* thus indicating the relative size of the supposed males and females. *Proagriocharis kimballensis* is smaller than any other turkey except *R. calobates*.

Proagriocharis kimballensis is most similar to *R. calobates, M. leopoldi,* and the Inglis fossils (Table 2). However, only the tarsometatarsi of *M. leopoldi* and *R. calobates* could be compared with *P. kimballensis*. In Table 3, *P. kimballensis* is seen to be most similar to *M. progenes* and *M. leopoldi,* although several other taxa are nearly as similar. In reporting a greater overall similarity of *Proagriocharis* to *Agriocharis* than to *Meleagris* (*gallopavo*) or *Parapavo* (*californicus*), Martin and Tate (1970) followed Brodkorb (1964a, b) in regarding *Agriocharis* as including the species *progenes, leopoldi, anza, crassipes,* and *ocellata,* of which *progenes* and *crassipes* are seen herein to be qualitatively the least similar of all turkeys to *Proagriocharis* (Table 2). *Meleagris progenes* and *M. crassipes* are, however, the most similar of the above to *P. kimballensis* in size. The H/A ratio of *P. kimballensis* is greater than that of all others (Table 22), but approaches that of *M. crassipes*.

In their generic diagnosis of the tarsometatarsus, Martin and Tate (1970) found *Proagriocharis* to differ from *Meleagris* (*gallopavo*) and *Parapavo* (*californicus*), but to resemble *Agriocharis* (*progenes, leopoldi, crassipes,* and *ocellata*), in having an angle of the spur core of less than 60 degrees. An increased sample size (Table 20: K) indicates that the spur core angle is not a generic character (see discussion on pages 139–40).

According to Martin and Tate (1970:215), "The spur core (cast) is more proximally placed (42 percent of the total length) than it is in *Agriocharis ocellata* (36 percent of the total length), and just overlaps the lower range of *Parapavo* [*californicus*] and *Meleagris* [*gallopavo*] in this respect." The relative height of the spur core of *P. kimballensis,* if based on their reported measurements (p. 217), would be 40.8 percent, as mentioned above, not 42 percent as reported. However, as Martin and Tate state, these measurements are from a cast and are therefore probably not extremely accurate. The figure of 40.8 percent is within the range found for numerous other forms (Table 22: G/A), and it is no basis for separating the species from other species at the generic level.

Martin and Tate (1970:217) distinguish *M. progenes* and *M. leopoldi* from *P. kimballensis* "because of the difference in the placement of the spur core in this species." I agree with them in the difference of the angle of spur core (Table 20: K), but find that the difference they report in the relative height of the spur core requires some clarification. It has been established above that the true height of the spur core of the single specimen of *P. kimballensis* is 40.8 percent, not 42 percent. They report the spur core of *M. leopoldi* (1970:217) to be "placed slightly lower (39.8 percent of the total length) than it is in *P. kimballensis* (see Miller and Bowman 1956:44)." They do not mention the fact that Miller and Bowman's ratio was based on the total length of the paratype and the height of the spur core of the holotype. Had Martin and Tate examined the paratype tarsometatarsus of *M. leopoldi,* a greater difference between it and *P. kimballensis* would have been seen (Table 22: G/A). Martin and Tate (1970:217) continue that the spur core of *M. progenes* is "slightly more distally placed than in *A. leopoldi*." This is true (Table 20: G), but it must be stressed that the *relative* height of the spur core in *M. progenes* from Rexroad, Kansas, is unknown, although it is 42.8 percent in a specimen of *Meleagris* cf. *M. progenes* from Benson, Arizona.

In summary, *Proagriocharis* is retained herein as a distinct genus, mainly because of its low similarity to most other forms as seen in Tables 2 and 3, although many characters used by Martin and Tate (1970) to distinguish it from other turkeys are shown to be invalid. As stated in the discussion of *Rhegminornis* above, *Proagriocharis* is probably not on or near the lineage leading to the larger Pleistocene and Recent forms of *Meleagris*. However, many more specimens of varying ages are needed before the relationships of *Proagriocharis* to earlier or later forms can be clearly stated.

BUCKHORN, Grant County, New Mexico. Meleagridinae, cf. *Meleagris*. Tibiotarsus (F:AM 10434)—Table 18. This specimen is from a form much larger than indicated for the known species of *Rhegminornis* and *Proagriocharis*. It is not qualitatively distinguishable from *Meleagris,* and it also resembles several species of *Meleagris* in size.

CLIFTON COUNTRY CLUB, Graham County, Arizona. Meleagridinae, genus and species indeterminate. Coracoid (F:AM 10421)—Table 4. This specimen, a humeral end of a coracoid, is similar in size to that of *Proagriocharis kimballensis,* if it represents a male. If it represents a female, it is similar in size to those of *M. californica, M. ocellata,* and *M. crassipes*. It resembles that of *P. kimballensis* in characters 7 and 10, but resembles the coracoids of all turkeys in characters 9, 13, 14 and 15. It differs from that of *P. kimballensis* in character 11, and is intermediate between that of *P. kimballensis* and other forms in character 17. Although agreeing with *M. crassipes* in all of its characters, this specimen cannot justifiably be referred to a known species.

BONE VALLEY (PALMETTO MINE), Polk County, Florida. Meleagridinae, cf. *Meleagris*. Distal end of tibiotarsus (UF 21033)—Table 19. No characters apparent other than size. This is the earliest definite record of a turkey in Florida, pending further elucidation of the affinities of *Rhegminornis*. This tibiotarsus and those from Westmoreland Park, Virginia, and Buckhorn, New Mexico, suggest a rather widespread occurrence of fairly large turkeys in the late Miocene and early Pliocene.

PLIOCENE (HEMPHILLIAN OR BLANCAN)

UNIVERSITY DRIVE, Orange County, California. *Meleagris* sp. Femur (LACM 64001)—Table 16. No characters apparent other than size. The primary significance of this specimen is that it documents the earliest known occurrence of a turkey in southern California.

LATE PLIOCENE (BLANCAN)

HAILE XVA, Alachua County, Florida. *Meleagris* sp. Tibiotarsus (UF 17545)—Table 18. No characters apparent other than size. Reported as *M. gallopavo* by Campbell (1976).

BENSON, Cochise County, Arizona. *Meleagris* cf. *M. progenes*. Tarsometatarsus (AMNH 6330, USNM 10551)—Tables 20, 22, Fig. 10; Fig. 5 of Wetmore (1924). USNM 10551 was referred to the genus *Agriocharis* by Wetmore (1924), while Brodkorb (1964b) referred this specimen to *A. progenes* because it was "similar in size and position of the spur core" (1964b:225). I have also examined a nearly complete tarsometatarsus from this site in which the spur core is broken. These specimens agree closely in size only with *M. progenes* from Rexroad, Kansas, and with *M. crassipes*. I refer them only tentatively to *M. progenes* because they are qualitatively separable only from *Rhegminornis calobates* (characters 14, 19) and *M. crassipes* (characters 5, 8, 16).

CITA CANYON, Randall County, Texas. *Meleagris leopoldi*. Tibiotarsus (PPHM 3174). Tarsometatarsus (PPHM 3169)—Tables 20, 22, Fig. 10; Fig. 1 of A. Miller and Bowman (1956). Reported as *Parapavo californicus* by L. Miller and Johnston (1937) and as cf. *Meleagris* by Johnston and Savage (1955), these specimens were described as a new species, *Meleagris leopoldi*, by A. Miller and Bowman (1956). Brodkorb (1964b) transferred *M. leopoldi* to *Agriocharis* on the basis of characters that are not considered herein to be of generic value, as detailed on pages 139–40 of the Comparative Osteology section.

Unfortunately, the tarsometatarsus is the only diagnostic element of *M. leopoldi* known from Cita Canyon. *Meleagris leopoldi* resembles rather closely all forms except *Rhegminornis*, *M. ocellata*, and *M. crassipes*, being closest to *M. progenes* (Table 3). The tarsometatarsus of *M. leopoldi* is consistently larger than that of *M. progenes*, although some degree of overlap would probably be seen if larger samples of each form were available. Potentially significant differences between *M. leopoldi* and *M. progenes* (specimens from both Rexroad and Benson considered) are seen in the B/E, E/A, and G/A ratios (Table 22). *Meleagris leopoldi* resembles specimens from Inglis in every measurement (Table 20) except A and E, the first of which can be extremely variable (note, for example, the range of all Recent specimens of *M. gallopavo* in Table 20). *Meleagris leopoldi* differs from *M. californica* in measurements E, F, and G (Table 20) and in the F/A and G/A ratios. *Meleagris leopoldi* is consistently smaller than *M. gallopavo* and differs in its G/A ratio. *Meleagris leopoldi* resembles *M. ocellata* in all measurements except D, and all ratios of these two forms are similar. *Meleagris leopoldi* is larger and of different proportions than *M. crassipes*.

It is seen from the comparisons above that the Cita Canyon specimen closely resembles both qualitatively and quantitatively only the Inglis specimens, although its high degree of qualitative similarity with *M. progenes* also suggests close affinities to that form. Considering the amount of variation seen in *M. gallopavo* in Table 20, it is quite likely that, if large samples of turkeys were available from Benson, Cita Canyon, and Rexroad, a case could be made for their conspecificity.

REXROAD, Meade County, Kansas. *Meleagris progenes*. All specimens have UMMP numbers. Premaxilla (31052). Mandible (47783). Sternum (31039). Coracoid (20940)—Table 4. Scapula (45930, 45965)—Table 7, Figure 9. Ulnare (48109). Carpometacarpus (20941, 48188)—Tables 14, 15. Femur (45912)—Table 16. Tibiotarsus (45970, 48191)—Table 19. Tarsometatarsus (31034, 48189)—Tables 20, 21, Figures 10, 14; Pl. I of Brodkorb (1964b). This species was described as *Agriocharis progenes* by Brodkorb (1964b) because of its supposed greater similarity to *M.* (*Agriocharis*) *ocellata* than to *M. gallopavo*. However, *M. progenes* shows no greater affinity to one of the living species than to another (Table 2). Nevertheless it is more similar to them than to either *Rhegminornis* or *Proagriocharis*, which supports its inclusion in the genus *Meleagris*. The apparent similarity between *M. progenes* and *M. leopoldi* seen in Table 3 is based only on the tarsometatarsus and thus may not be an accurate reflection of affinities (compare Table 2 to Table 3). *M. progenes* is of a size that may be distinct from all other forms except *M. crassipes*, to which it does not show enough qualitative resemblance to suggest a close relationship.

EARLY PLEISTOCENE (IRVINGTONIAN)

GILLILAND, Knox County, Texas. Meleagridinae, genus and species indeterminate. Coracoid (PB unnumbered)—Table 5. Femur (UMMP 39387)—Table 17; Pl. I of Brodkorb (1964b). No characters other than size are apparent in the badly crushed coracoid from the Bruce Burnett Ranch. The femur from Rattlesnake Point, reported as *Agriocharis* sp. in Hibbard (1960), was referred to *M.* (*Agriocharis*) *anza* by Brodkorb (1964b:228) on the basis of "agreement in geologic horizon, general size, and marked expansion of the shaft of the femur (shaft of humerus expanded in type of *A. anza*)." I have not examined this specimen, but do not consider it safely referable to *M. anza* for the following reasons: (1) chronological agreement is not a sound basis for biological relationship; (2) agreement in size is not guaranteed because of the uncertainty of the sex of the specimens involved; (3) a mediolateral expansion of the shaft of the femur is not known to be related to such an expansion in the humerus (in the case of the Vallecito Creek specimen, the expansion is due to crushing); (4) as noted by Brodkorb (1964b), no femur is known from Vallecito Creek, making direct comparison of specimens impossible. As neither the coracoid nor the femur from Gilliland are large enough to be safely referable to *Meleagris*, no generic allocation is made.

INGLIS IA, Citrus County, Florida. *Meleagris* cf. *M. leopoldi* or *M. anza*. All specimens have UF numbers. Numbers in parentheses are numbers of specimens examined. Individual catalogue numbers available on request. Cranium (9). Premaxilla (1). Quadrate (8). Mandible (7). Basihyal (1). Axis (5). Cervical Vertebra (128). Sixth Thoracic Vertebra (12). Fused Thoracic Vertebrae (24). Synsacrum (41). Caudal Vertebra (6). Pygostyle (3). Vertebral Rib (32). Sternal Rib (14). Sternum (26). Furcula (5)—Figure 8. Coracoid (67)—Tables 4, 5. Scapula (34)—Tables 8, 9, Fig. 9. Humerus (94)—Tables 12, 13. Ulna (73)—Tables 10, 11. Radius (46)—Tables 12, 13. Ulnare (10). Radiale (8). Carpometacarpus (49)—Tables 14, 15. Pollex (11). Manus Digit II, Phalanx I (24). Manus Digit II, Phalanx II (10). Manus Digit III (4). Pelvis (31). Femur (81)—Tables 16, 17. Patella (1). Tibiotarsus (93)—Tables 18, 19. Fibula (28). Tarsometatarsus (108)—Tables 20–22, Figs. 10, 12, 14. Hallux (6). Pes Digit I, Phalanx I (6). Pes Digit II, Phalanx I

(13). Pes Digit II, Phalanx II (13). Pes Digit III, Phalanx I (24). Pes Digit III, Phalanx II (13). Pes Digit III, Phalanx III (11). Pes Digit IV, Phalanx I (13). Pes Digit IV, Phalanges II, III, IV (28). Ungual Phalanx (16). Misc. Pedal Phalanx (3). Known from about 1240 specimens, this is the earliest turkey for which any appreciation of individual variation can be attained. Previously (Steadman 1975), and with much hesitation, I referred the Inglis fossils to *M. anza* because the humeri could not be distinguished from the poorly preserved holotype of *M. anza*. However, as already noted, the tarsometatarsus of *M. leopoldi* also bears much resemblance to those from Inglis, and the two populations may represent a single species. Again I am faced with the problem of referring a large series of specimens to a species known essentially from one element. *Meleagris leopoldi* is based on a tarsometatarsus (unknown in *M. anza*), a very diagnostic and commonly preserved element of turkeys. As the tarsometatarsus is spurred, we can be reasonably sure that the known specimens of *M. leopoldi* represent males, thereby also providing an idea of the size of the females. That a strong sexual dimorphism in size was developed even before the time of *M. leopoldi* is shown by the carpometacarpus and tarsometatarsus of *M. progenes*. Although the holotype humerus of *M. anza* equals those of females from Inglis in size, the possibility exists that it actually represents a male of a very small species. Referral of the Inglis specimens to either *M. leopoldi* or *M. anza* is somewhat tentative, each species being based on specimens of only one skeletal element. However, I consider this action to be better than describing the turkey from Inglis as a new species, thereby adding another name of dubious validity to the already excessively long list of specific names of turkeys. I believe that future discoveries of turkeys of ages similar to those of Cita Canyon, Inglis, and Vallecito Creek may show that the turkeys from these sites represent one lineage that slowly increased in size through time. In this case, the delimitation of species would be arbitrary, and *M. leopoldi* and *M. anza* might even be regarded as conspecific. That a single species of turkey could have such a wide geographical range is not at all surprising when one considers the present range of *M. gallopavo* and the diverse types of habitat that it occupies. If new fossils prove that the turkeys from Inglis are distinct from those of Cita Canyon or Vallecito Creek, appropriate nomenclatural steps can be taken at that time.

Closest affinities of the turkey from Inglis appear to be with fossils from Coleman; and it is least similar to *Rhegminornis calobates, Meleagris gallopavo,* and *M. ocellata* (Table 2). As shown in Table 3, the greatest resemblance is with *M. progenes* and fossils from Coleman, with only *R. calobates* being very dissimilar. The Inglis turkey is larger in size than *R. calobates, P. kimballensis, M. progenes, M. ocellata,* and *M. crassipes*; equal to or slightly larger than *M. leopoldi* or *M. californica*; slightly smaller than the population from Coleman; smaller than *M. gallopavo*.

Distinctive ratios of the Inglis fossils in Table 22 include the following: G/A is less than in all other forms except *M. leopoldi*; J/A is greater than in all forms except Coleman specimens and *M. ocellata*; K/A is less than in all forms except *M. crassipes*; P/A is less than in all forms except *M. g. osceola*.

Were it not for the series of intermediate fossils from Coleman, the degree of difference between the Inglis fossils and *M. gallopavo* apparent from Table 2 would suggest a possible sudden replacement of the early *leopoldi-anza*-like form by the larger *gallopavo* at some point in the Pleistocene. It now appears that the Florida peninsula, if not much of the southern portion of North America, has been occupied since at least Blancan times by a series of populations of turkeys that increased slightly in size through time.

The turkey from Inglis possesses certain features, such as the stout furcula and the non-pneumatic scapula, that are thus far unknown in any later forms. The evolutionary implications of these structures will be discussed in the section on evolution.

VALLECITO CREEK, San Diego County, California. *Meleagris anza.* All are LACM 3753. Sternum. Humerus—Table 9; Pl. III in Howard (1963). Ulna. Synsacrum. This material was described as a new species, *Agriocharis anza,* by Howard (1963), with a humerus as the holotype. Unfortunately, specimens other than the humerus are damaged beyond usefulness. The holotype humerus is crushed more severely on the anconal side than on the palmar side. I consider its broad, flat shaft (Table 9: C, D) and deep brachial depression (character 9) to be due to this crushing, a possibility recognized by Howard (1963). I also regard the curvature of the shaft (character 8) as an artificial condition. Therefore, characters 8 and 9 are not considered in compiling Table 2, in which the humerus from Vallecito Creek is seen to be slightly closer to Inglis specimens and those of *M. gallopavo* than to those of other forms. Based upon only seven characters of just one element, these figures may be of little value. The holotype of *M. anza* differs from other forms in the following qualitative characters: Coleman specimens—character 12; *M. gallopavo*—character 12; *M. californica*—characters 10, 12; *M. ocellata*—characters 5, 7, 12; *M. crassipes*—characters 7, 12. It cannot be distinguished from humeri from Inglis by any of these characters. In referring this humerus to *Agriocharis* instead of *Meleagris,* Howard's (1963) characters included the shape of the external condyle (character 13), now known to be variable and therefore of little value, and the orientation of the attachment of M. pronator brevis (character 10), which varies in some forms, but appears to be consistent in others. This single specimen cannot provide any indication of individual variation of its population.

Except for the width and depth of the shaft, which are altered by crushing, this specimen resembles in size the females of several different forms. If the material from Vallecito Creek had not already been the basis for the description of a new taxon, I would have called the material "Meleagridinae, cf. *Meleagris*." As this material cannot be clearly distinguished quantitatively from several species of *Meleagris,* its tentative referral to *Meleagris* would seem justified. However, as the available specimens from Vallecito Creek represent the type material of *Meleagris anza,* instead of regarding this name as a *nomen dubium,* I retain it with the hope that more diagnostic specimens will be recovered at this site in the future. An effective suite of characters simply cannot be based on poorly preserved material of only one or several elements, especially when dealing with such intraspecifically variable organisms as turkeys. Diagnoses based on single specimens of variable organisms cannot account for individual variation and will almost surely be altered by the discovery of new specimens. The old idea that avian fossils are very rare has promoted descriptions of "species" based on material that is often at best indicative only of a family or genus, thereby forcing future workers either to tentatively refer similar new fossil material to the poorly defined taxon, or else not recognize the old taxon. Only through the discovery of new, more diagnostic fossils at Vallecito Creek can the true affinities of *M. anza* be learned.

PORT KENNEDY CAVE, Montgomery County, Pennsylvania. Meleagridinae cf. *Meleagris*. Carpometacarpus (ANSP 165)—Table 14. Without naming the element(s) involved, Wheatley reported "a turkey" (1871a:237) and "*Meleagris* ——?" (1871b:385) from this site. Mercer (1899:280) included "*Meleagris altus,* leg bone with spur" in his faunal list of Port Kennedy Cave, noting that the single specimen was excavated by Wheatley in 1871. The location of this specimen is unknown to me. Wetmore (1931b) listed this record as *M. superba* (= *alta*) as did Brodkorb (1964a), under the name *M. alta*. The only fossil of a turkey from this site that I have examined is a previously unreported complete carpometacarpus, which differs from those of Inglis, Coleman, and *M. gallopavo* in having metacarpal I less protrudent anteriorly, although several specimens from Inglis closely approach its condition. It is larger than females of any species, and, if it represents a male, it is the size of those of Inglis, Coleman, or *M. californica,* being slightly smaller than in *M. gallopavo*.

The exact affinities of this specimen cannot be determined from the available data. Although resembling *Meleagris* in size, it differs from this genus in its small metacarpal I. Generic characters of the carpometacarpus of turkeys are at present undetermined, as this element is unknown in *Rhegminornis* or *Proagriocharis*.

HAILE XVI A, Alachua County, Florida. *Meleagris* sp. Scapula (UF 22083, 22084)—Table 7. Humerus (UF 22081, 22082)—Table 8. Femur (UF 22086). Tibiotarsus (UF 22085). Pedal Phalanx (UF 22087). The scapulae have a pneumatic foramen, thus resembling post-Inglis forms. They agree in size with the Coleman fossils more than with the Inglis form or *M. g. osceola*. The distal end of a humerus shows no characters other than size, in which it resembles Inglis specimens more than the Coleman fossils or *M. gallopavo*.

These fossils are referred to *Meleagris,* but not to any species, on the basis of the above characters. These specimens suggest a form of turkey between those of Inglis and Coleman if one assumes that the same lineage is involved. A refinement of the age of this site is expected once the mammalian fauna is studied further. This will help to pinpoint the time of the development of the pneumatic foramen in the scapula.

WILLISTON, Levy County, Florida. *Meleagris* sp. Femur (PB 2321). No characters apparent other than size. Reported as *M. gallopavo* by Holman (1959:5) and Brodkorb (1964a:335).

COLEMAN IIA, Sumter County, Florida. *Meleagris* sp. (intermediate between *leopoldi-anza* and *gallopavo*). All specimens have UF numbers. Numbers in parentheses are numbers of specimens examined of each element. Individual catalogue numbers available on request. Cranium (3). Premaxilla (1). Axis (2). Cervical Vertebra (53). Sixth Thoracic Vertebra (4). Fused Thoracic Vertebra (1). Synsacrum (7). Sternal Rib (2). Sternum (12). Coracoid (18)—Tables 4, 5. Scapula (6)—Tables 6, 7, Fig. 9. Humerus (37)—Tables 8, 9. Ulna (23)—Tables 10, 11. Radius (9)—Tables 12, 13. Radiale (1). Carpometacarpus (12)—Tables 14, 15. Manus Digit II, Phalanx I (2). Manus Digit II, Phalanx II (2). Pelvis (7). Femur (27)—Tables 16, 17. Tibiotarsus (33)—Tables 18, 19. Tarsometatarsus (35)—Tables 20–22, Figs. 10, 12, 14. Pes Digit II, Phalanx I (4). Pes Digit III, Phalanx I (8). Pes Digit III, Phalanx II (2). Pes Digit III, Phalanx III (1). Pes Digit IV, Phalanx I (1). These 320 fossils provide a link between the older *M. leopoldianza*-like forms and the younger *M. gallopavo* and *M. californica*. I noted previously (Steadman 1975) an intermediateness between the Inglis fossils and later forms and referred the Coleman fossils to *M. anza,* thereby attempting to stress their similarity to the Inglis fossils. Although showing a slightly greater overall resemblance to the Inglis specimens than to those of *M. gallopavo* or *M. californica,* the Coleman fossils are not herein regarded as conspecific with those from Inglis since a distinct change, the attainment of a pneumatic foramen in the scapula, occurred in the interval between deposition of the Inglis and Coleman faunas. In the absence of the Coleman specimens, the relatively low amount of similarity of the specimens from Inglis to *M. gallopavo* (Table 2) would suggest a more distant relationship than is proposed herein. The Coleman turkey shows less similarity to *M. ocellata* or *M. crassipes* than to *M. progenes, M. gallopavo,* or *M. californica* (Table 2). Its lowest similarity is with *Rhegminornis calobates* and *Proagriocharis kimballensis*.

The Coleman specimens are definitely larger in overall size than those of *Rhegminornis calobates, Proagriocharis kimballensis, M. progenes,* or *M. crassipes*; almost always larger than those of *M. ocellata*; usually larger than Inglis specimens or *M. californica,* overlapping more with the former than with the latter; and usually smaller than those of *M. gallopavo,* often with overlap.

Distinctive ratios of the Coleman specimens in Table 22 are as follows: B/E is greater than in Inglis specimens; J/A is greater than in all others except Inglis specimens and *M. ocellata*. A general trend in these ratios is the relative stoutness of the Coleman specimens as compared to *M. g. osceola*. In every case, however, specimens from Rancholabrean sites in Florida either more strongly resemble Coleman specimens than those of *M. g. osceola,* or are intermediate, providing further evidence that the Coleman form was directly ancestral to *M. gallopavo*.

SANTA FE RIVER IIA, Gilchrist County, Florida. *Meleagris* cf. *M. gallopavo*. Ulna (UF 14930)—Table 10. Femur (UF 14928)—Table 16. Tibiotarsus (UF 22078)—Table 18. Tarsometatarsus (UF 22076, 22077)—Tables 20, 22. These specimens resemble specimens of late Rancholabrean and Recent *M. gallopavo* more closely than those of Inglis or Coleman in size and H/C ratio (Table 22). However, the tarsometatarsus differs from that of *M. gallopavo* in character 4.

LATE PLEISTOCENE (RANCHOLABREAN)

RANCHO LA BREA, Los Angeles County, California. *Meleagris californica*. All specimens from LACM. Numbers in parentheses are numbers of specimens of each element examined. Individual catalogue numbers available on request. Cranium (2). Premaxilla (3). Mandible (2). Fused Thoracic Vertebrae (1). Synsacral Vertebra (1). Pygostyle (1). Sternum (4). Furcula (4). Coracoid (56)—Tables 4, 5. Scapula (51)—Tables 6, 7, Fig. 9. Humerus (65)—Tables 8, 9. Ulna (64)—Tables 10, 11. Radius (74)—Tables 12, 13. Carpometacarpus (64)—Tables 14, 15. Pelvis (4). Femur (105)—Tables 16,

17. Tibiotarsus (74)—Tables 18, 19. Fibula (4). Tarsometatarsus (82)—Tables 20–22, Figs. 12, 14; Plate 25 of L. Miller (1909); Figs. 44, 45 of L. Miller (1940). All major elements illustrated in Pls. 1–13 of Howard (1927). L. Miller (1909) described this species as *Pavo californicus,* a phasianine. L. Miller (1916a) later erected the genus *Parapavo* for these specimens, which he regarded (L. Miller 1916a, 1916b, 1925) as being intermediate between *Pavo* and *Meleagris ocellata,* and more closely related to these two species than to *M. gallopavo*. Interestingly, L. Miller (1912:78) included "*Meleagris?*" alongside *Pavo californicus* in a list of birds from Rancho La Brea, with no mention of the elements involved. Wetmore (1924), referring only to a tarsometatarsus, regarded *Parapavo* not as a peacock but as a turkey intermediate between *Agriocharis* (*ocellata*) and *Meleagris* (*gallopavo*), although closer to the latter. After a very thorough study of *Parapavo,* Howard (1927) agreed with Wetmore (1924), except for considering *Parapavo* more closely related to *Agriocharis* than to *Meleagris*. Although Howard (1927) considered *Parapavo* to be generically separable from *Meleagris gallopavo* and *M. ocellata,* only in the fibula did she find *M. californica* to be consistently generically distinct from both *M. gallopavo* and *M. ocellata,* although noting (Howard 1927:24) "Owing to the variability in the fibula of *Pavo* and *Agriocharis,* little import can be attached to this element." Howard (1928), with a study of the premaxilla, gave support to her previous conclusion that *Parapavo* is different at the generic level from other turkeys. Sushkin (1928), comparing the coracoid, carpometacarpus, and tarsometatarsus of *M. californica* with those of *M. ocellata* and *Pavo,* concluded that *M. californica* is not related to *Pavo* but is sufficiently similar to *M. ocellata* that it could be congeneric. Wetmore (1931b), L. Miller (1942) and Brodkorb (1964a, b) all recognized *Parapavo,* while A. Miller and Bowman (1956) found no basis for a generic distinction in the tarsometatarsi of *Meleagris* and *Parapavo*.

Analysis of the various supposed generic characters of the turkey from Rancho La Brea is provided in the "Comparative Osteology" section, where *M. californica* is seen to lack characters that warrant generic separation from *M. gallopavo* or *M. ocellata*. *Meleagris californica* is not an unusual form at all, but simply another species of *Meleagris* with rather close affinities to other species of the genus (Tables 2 and 3), which it also resembles in size. Thus, I consider the genus *Parapavo* L. Miller to be a synonym of *Meleagris* Linnaeus.

IMPERIAL HIGHWAY (LACM 1052), Orange County, California. *Meleagris* sp. Radius (LACM 1052/2009)—Table 12. No characters apparent other than size. Referred to *Parapavo californicus* by Howard (1936) on the basis of characters herein regarded as inconsistent (see page 135). Also reported as *P. californicus* by L. Miller (1942), Brodkorb (1964a), and W. Miller (1971). L. Miller (1942) and Brodkorb (1964a) refer to this site as La Habra, California.

CARPINTERIA, Santa Barbara County, California. *Meleagris californica*. All specimens are LACM. Numbers in parentheses are numbers of specimens examined of each element. Individual catalogue numbers available on request. Coracoid (17)—Tables 4, 5. Scapula (10)—Tables 6, 7. Humerus (17)—Tables 8, 9. Ulna (22)—Tables 10, 11. Radius (16)—Tables 12, 13. Carpometacarpus (17)—Tables 14, 15. Femur (16)—Tables 16, 17. Tibiotarsus (21)—Tables 18, 19. Tarsometatarsus (16)—Tables 20–22. There are no significant qualitative or quantitative differences between these specimens and those of *M. californica* from Rancho La Brea. Reported as *Parapavo californicus* by L. Miller (1927, 1942), Wetmore (1931b), and Brodkorb (1964a).

WORKMAN AND ALHAMBRA STREETS (LACM 1023), Los Angeles County, California. Meleagridinae, cf. *Meleagris*. Tibiotarsus (LACM 982)—Table 19. No characters apparent other than size. Howard (1936:250) found that this specimen "may be assignable to *Parapavo,* but unfortunately they do not possess any diagnostic generic characters by which to make definite identification." Reported as *Parapavo californicus* by L. Miller (1942) and Brodkorb (1964a), and as cf. *Parapavo* by W. Miller (1971:55), who called this site "Workman and Alameda Sts."

LA MIRADA, Los Angeles County, California. *Meleagris* cf. *M. californica*. Radius (LACM 2009)—Table 12. No characters apparent other than size. W. Miller (1971) referred a partial coracoid (not examined by me) and the radius from this site to *Parapavo californicus*.

POTTER CREEK CAVE, Shasta County, California. *Meleagris* sp. Coracoid (UCMP 1055/8368)—Table 5. Humerus (UCMP 1055/114545)—Table 9. Qualitatively separable from all species except *M. gallopavo* and *M. californica,* each of these specimens may also resemble either of the above two species in size. Reported as *Meleagris* sp. by L. Miller (1911); as "referable either to *Parapavo* or to *Meleagris*" by L. Miller (1925:67); and as *Parapavo californicus* by Brodkorb (1964a). Mention is made here of the report of "*Meleagris* sp." from Hawver Cave, Eldorado County, California, by L. Miller (1912:75). I have not located the specimen involved, nor were any turkeys reported from Hawver Cave by L. Miller (1911) or Brodkorb (1964a).

AMERICAN FALLS, Power County, Idaho. *Meleagris gallopavo*. Tarsometatarsus (ISUM 1736)—Tables 20, 22. Reported also as *M. gallopavo* by Hopkins et al. (1969), this specimen agrees with tarsometatarsi of *M. gallopavo* in size, proportions, and in all characters except no. 4.

PAPAGO SPRINGS CAVE, Santa Cruz County, Arizona. *Meleagris* sp. Humerus (AMNH 8683, 8687)—Table 9. Femur (AMNH 8684, 8685)—Table 17. These specimens are indistinguishable from females of *M. gallopavo* or males of *M. crassipes*. North Papago Cave, which is an extension of Papago Springs Cave, contained a tarsometatarsus of *M. crassipes* (Rea this vol.).

ARIZPE, Sonora, México. *Meleagris* cf. *M. gallopavo*. Humerus (AMNH 6823)—Table 8. No character apparent other than size. Reported as *M. gallopavo* by Cracraft (1968). Also regarded as *Meleagris* cf. *M. gallopavo* by Rea (this vol.).

BURNET CAVE, Eddy County, New Mexico. *Meleagris* cf. *M. gallopavo*. Humerus (ANSP 14161)—Table 8. Carpometacarpus (ANSP 13495)—Table 15. Femur (ANSP 14134)—Table 17. Tibiotarsus (ANSP 14133)—Table 19. No characters apparent other than size. Reported as *M. gallopavo* by Schultz and Howard (1935). Although the humerus is too large for *M. crassipes,* a tarsometatarsus referable to *M. crassipes* has also been recovered from Burnet Cave (Rea this vol.). The stratigraphic positions of the various fossils of turkeys from Burnet Cave are unknown.

MELBOURNE, Brevard County. *Meleagris* cf. *M. gallopavo*. Scapula (USNM 17035, 17036)—Table 7. Humerus (USNM 12123)—Table 8. Ulna (USNM 12113). Carpometacarpus (USNM 17028, 17038, 17039)—Tables 14, 15. Tibiotarsus (USNM 12114, 17034). Tarsometatarsus (USNM 12108, 17037, 17040)—Table 20. No characters apparent other than size. Reported as *M. gallopavo* by Wetmore (1931a, b) and Brodkorb (1964a).

ARREDONDO, Alachua County. *Meleagris* cf. *M. gallopavo*. Humerus (PB 1630)—Table 8. No characters apparent other than size. Reported as *M. gallopavo* by Brodkorb (1959, 1964a).

SABERTOOTH CAVE, Citrus County. *Meleagris* cf. *M. gallopavo*. Tarsometatarsus (USNM 12188)—Tables 20, 22. No characters apparent other than size. Reported as *M. gallopavo* by Wetmore (1931a, b) and Brodkorb (1964a).

AUCILLA RIVER IA, Jefferson County. *Meleagris gallopavo*. Humerus (USNM 209602)—Table 8. Radius (USNM 209709)—Table 12. Tibiotarsus (USNM 209607, 209705)—Tables 18, 19. Tarsometatarsus (USNM 209605, 209609)—Tables 20, 22. Referral of these specimens to *M. gallopavo* is based on size and proportions of the tarsometatarsus, in which they differ from those of Inglis or Coleman.

ICHETUCKNEE RIVER, Columbia County. *Meleagris gallopavo*. All specimens have either UF or PB numbers. Numbers in parentheses are numbers of specimens examined. Individual catalogue numbers available on request. Sternum (1). Coracoid (11)—Tables 4, 5. Scapula (1)—Table 7. Humerus (11)—Tables 8, 9. Ulna (9)—Tables 10, 11. Radius (1)—Table 12. Carpometacarpus (14)—Tables 14, 15. Femur (8)—Tables 16, 17. Tibiotarsus (37)—Tables 18, 19. Tarsometatarsus (44)—Tables 20–22. This large series of fossils generally agrees very closely with specimens of Recent *M. gallopavo* and differs in many ways from the fossils from Inglis or Coleman. They usually resemble *M. g. silvestris* in size and proportions more than *M. g. osceola*. Reported as *M. gallopavo* by Wetmore (1931a, b), McCoy (1963), Brodkorb (1964a), and Campbell (this vol.).

KENDRICK IA, Marion County. *Meleagris* sp. Tibiotarsus (PB 1410)—Table 19. Tarsometatarsus (PB 1409)—Table 20. These fragmentary specimens resemble *M. gallopavo* except in character 4 of the tarsometatarsus. Reported as *M. gallopavo* by Brodkorb (1964a).

VERO, Indian River County. *Meleagris* cf. *M. gallopavo*. Carpometacarpus (PB 8467)—Table 15. No characters apparent other than size. Shufeldt (1917) unknowingly was the first to report a turkey from Vero, describing the worn distal half of a meleagridine tibiotarsus as *Ardea sellardsi*, a supposed new species of heron. Wetmore (1931a) recognized Shufeldt's interordinal error and synonymized *Ardea sellardsi* with *Meleagris gallopavo*, and also reported several other specimens from this site as *M. gallopavo*. Also listed as *M. gallopavo* by Wetmore (1931b) and Brodkorb (1964a).

SEMINOLE FIELD, Pinellas County. *Meleagris gallopavo* (includes the synonym *M. tridens*). All are USNM 244387 except a humerus (USNM 12207), a tibiotarsus (USNM 12214), and a tarsometatarsus (USNM 12052). Numbers in parentheses are numbers of specimens examined. Coracoid (3)—Tables 4, 5. Scapula (1)—Table 7. Humerus (3)—Tables 8, 9. Ulna (7)—Tables 10, 11. Carpometacarpus (10)—Tables 14, 15. Femur (8)—Tables 16, 17. Tibiotarsus (7)—Tables 18, 19. Tarsometatarsus (28)—Tables 20–22, Fig. 13; Fig. 13 of Wetmore (1931a). This series of fossils, reported as *M. gallopavo* (all specimens except USNM 12052) and *M. tridens* Wetmore (USNM 12052 only) by Wetmore (1931a, b) and Brodkorb (1964a), agrees qualitatively and quantitatively with specimens of Recent *M. gallopavo*. Brodkorb (1964a) noted that *M. tridens* may merely be a specimen of *M. gallopavo* with an abnormal development of three tarsal spurs. Williams (1967) documented the occurrence of double spurs in living *M. g. osceola* from Florida. There is also a tarsometatarsus from Inglis (UF 20680) with two spurs. Figure 13 illustrates the holotype of *M. tridens* next to a specimen of *M. g. osceola* with three spurs, and a specimen of *M. ocellata* with two spurs. I agree with Wetmore (1931a) in noting the lack of differences other than the aberrant spurs between *M. tridens* and *M. gallopavo*. *Meleagris tridens* is therefore a synonym of *M. gallopavo*.

Mention may be made here of a record of *M. gallopavo* at "Pleistocene cavern deposits at Ocala, Florida" by Shufeldt (1918:358; for further references to this site, see Ray 1957). These specimens could not be located at the United States National Museum, where Shufeldt said they would probably be deposited. Pending re-examination of these specimens, this record should not be considered as a valid occurrence of *M. gallopavo*.

The following are 13 Pleistocene localities in Florida whose faunas are either very limited or unstudied. All are regarded herein as Rancholabrean (M. Frazier and S.D. Webb pers. comm.), an age that is not refuted by the turkey specimens from these sites. Because their ages are not as refined as the other Floridian sites discussed above, they are simply listed in alphabetical order.

BOWMAN IA, Putnam County. *Meleagris* cf. *M. gallopavo*. Tarsometatarsus (PB 8606)—Tables 20, 22. No characters apparent other than size.

DAVIS QUARRY, Citrus County. *Meleagris gallopavo*. Coracoid (UF 22702, 22703)—Table 4. Femur (UF 22074)—Table 16. These specimens agree with those of *M. gallopavo* in all ways, and differ from specimens from Inglis and Coleman in character 11 of the coracoid.

ECONFINA RIVER, Taylor County. *Meleagris* sp. Tibiotarsus (USNM 243754)—Table 19. No characters apparent other than size.

FLORIDA LIME COMPANY, Marion County. *Meleagris* sp. Coracoid (PB 8439)—Table 5. Radius (PB 8440)—Table 12. Carpometacarpus (PB 8441, 8442)—Table 14. The coracoid resembles those from Coleman, not those of Recent *M. gallopavo*, in character 1, while the opposite is true in character 10. No other characters are apparent. Reported as *M. gallopavo* by Brodkorb (1964a).

HAILE IIA. Alachua County. *Meleagris* cf. *M. gallopavo*. Ulna (PB 1577)—Table 10. Tarsometatarsus (PB 1575). No characters apparent other than size. Reported as *M. gallopavo* by Brodkorb (1964a).

HOG CREEK, Sarasota County. *Meleagris* sp. Femur (USNM 12096)—Table 17. Tibiotarsus (USNM 12098)—Table

19. No characters apparent other than size. Reported as *M. gallopavo* by Wetmore (1931a, b) and Brodkorb (1964a).

MEFFORD CAVE I, Marion County. *Meleagris* cf. *M. gallopavo*. All are UF 2119. Premaxilla. Mandible. Coracoid—Table 4. Scapula—Table 7. Ulna—Table 10. Radius—Table 12. Carpometacarpus—Table 14. Synsacrum. Pelvis. These elements agree with those of Recent *M. gallopavo* in all respects except that the premaxilla is wider.

OAKHURST QUARRY, Marion County. *Meleagris* sp. Tibiotarsus (PB 8495)—Table 18. No characters apparent other than size.

ST. MARK'S RIVER, Leon and Wakulla Counties. *Meleagris* sp. Femur (USNM 209922)—Table 16. Tibiotarsus (USNM 209921). No characters apparent other than size.

SANTA FE RIVER IA, Gilchrist County. *Meleagris* cf. *M. gallopavo*. Femur (UF 22080)—Table 17. Tibiotarsus (UF 10664)—Table 18. Tarsometatarsus (UF 10667)—Tables 20, 22. Although these specimens lack qualitative distinctions, their size and proportions, especially of the tarsometatarsus, are more similar to those of Recent *M. gallopavo* than to those of Inglis or Coleman fossils. This site contains a mixture of Blancan and Rancholabrean fossils (Webb 1974), but the turkey fossils are regarded herein as Rancholabrean because of their similarity to *M. gallopavo*. These are probably the same specimens as those upon which Brodkorb (1963) reported *M. gallopavo* from Santa Fe I.

SANTA FE RIVER IVA, Gilchrist County. *Meleagris* sp. Ulna (UF 16806)—Table 10. Femur (UF 22079). Tibiotarsus (UF 16806, 22079)—Tables 18, 19. No characters apparent other than size.

STEINHATCHIE RIVER, Taylor and Dixie Counties. *Meleagris* cf. *M. gallopavo*. Radius (USNM 243755)—Table 12. No characters apparent other than size.

WEKIVA RUN III, Levy County. *Meleagris* sp. Tibiotarsus (UF 14214)—Table 18. No characters apparent other than size.

HOLOCENE

WACISSA RIVER, Jefferson County, Florida. *Meleagris gallopavo*. Tarsometatarsus (USNM 239842)—Tables 20, 22. This specimen differs from those of Inglis and Coleman and agrees with Recent *M. gallopavo* in size and proportions.

NICHOL'S HAMMOCK, Dade County, Florida. *Meleagris gallopavo*. All are UF 22075. Numbers in parentheses are numbers of specimens examined. Coracoid (5)—Tables 4, 5. Scapula (1)—Table 9. Ulna (5)—Table 11. Radius (1)—Table 12. Carpometacarpus (3)—Tables 14, 15. Femur (2)—Table 17. Tibiotarsus (8)—Tables 18, 19. Tarsometatarsus (3)—Table 21. This series agrees in every way with specimens of Recent *M. gallopavo,* being more similar in size to those of *M. g. osceola* than to those of late Pleistocene *M. gallopavo,* such as from Ichetucknee River. Reported as *M. gallopavo* by Hirschfeld (1968).

GOOD'S SHELLPIT, Volusia County, Florida. *Meleagris gallopavo*. Coracoid (PB 1709, 2163)—Tables 4, 5. Humerus (PB 1646, 1723, 1734, 1776)—Tables 8, 9. Ulna (PB 1757, 1828)—Tables 10, 11. Carpometacarpus (PB 1617, 1725)—Tables 14, 15. Femur (PB 1698, 1710, 1735, 1777, 1810)—Tables 16, 17. Tibiotarsus (PB 1758, 1778)—Tables 18, 19. These specimens agree in every way with those of Recent *M. gallopavo*. Reported as *M. gallopavo* by Brodkorb in Neill et al. (1956) and by Brodkorb (1964a).

SILVER GLEN SPRINGS, Lake County, Florida. *Meleagris* sp. Femur (PB 8498, 8499)—Table 16. No characters apparent other than size. Reported as *M. gallopavo* by Brodkorb in Neill et al. (1956) and Brodkorb (1964a).

BUFFALO SITE, Putman County, West Virginia. *Meleagris gallopavo*. All specimens are SBU. Numbers in parentheses are numbers of specimens examined. Individual catalogue numbers available on request. Coracoid (234)—Tables 4, 5. Scapula (30)—Tables 6, 7. Humerus (277)—Tables 8, 9. Ulna (116)—Tables 10, 11. Radius (69)—Tables 12, 13. Carpometacarpus (308)—Tables 14, 15. Femur (63)—Tables 16, 17. Tibiotarsus (113)—Tables 18, 19. Tarsometatarsus (131)—Tables 20–22. All major elements are illustrated in Figs. 1–10 of Kooliath (1975). This large series of bones, although representing birds eaten by 17th century Amerindians, are regarded by Kooliath (1975) and me as representing a wild population of *M. gallopavo*. They thus provide an unexcelled sample of *M. g. silvestris* from the period prior to extensive contact with Europeans. These bones were measured and described by Kooliath (1975), who compared them with modern *M. g. silvestris* from New York, finding the modern birds to be 2 to 3 percent smaller in all linear measurements (generally only total length considered) than those of AD 1650. My data include more types of measurements on a larger number of bones and yield the same slight difference in size. Kooliath suggested that selection for increased wildness because of increased hunting pressure since European contact may be the main factor leading to the apparent reduction in size.

HARTMAN'S CAVE, Monroe County, Pennsylvania. *Meleagris gallopavo*. Coracoid (ANSP 761)—Table 4. Humerus (ANSP 758–760, 771)—Tables 8, 9. Carpometacarpus (ANSP 753)—Table 14. Tibiotarsus (ANSP 753)—Table 19. Tarsometatarsus (ANSP 753)—Tables 20–22. Originally reported as *M. gallopavo* by Leidy (1889), who noted that this deposit, apparently collected without any stratigraphic control, contained extinct genera of mammals (*Mylohyus, Castoroides*) as well as advanced Amerindian artifacts, including ceramics. Although Leidy (1889) gave no provenience for the turkey bones contained therein, this site is listed as a Pleistocene record for *M. gallopavo* by both Wetmore (1931b) and Brodkorb (1964a). Upon examination of the specimens involved, I discovered that some of the turkey bones not only bear butcher marks made from steel knives, but also have obviously been shot by a shotgun, lead pellets from which are still contained within several of the bones. Thus Hartman's Cave can no longer be regarded as a Pleistocene locality for *M. gallopavo*. The lack of mineralization of these bones further supports their recency of deposition, as does the fact that they are inseparable from modern skeletons of *M. gallopavo*. The alternative hypothesis of Pleistocene firearms is rejected.

HOLOCENE MAYAN ARCHAEOLOGICAL SITES

DZIBILCHALTÚN, Yucatán, México. *Meleagris ocellata*. All specimens have UFZA numbers. Coracoid (31 M-101, 603

M-825, 726 M-626)—Tables 4, 5. Humerus (728 M-567, 172 M-101)—Table 8. Ulna (M-110, 339 M-176)—Table 10. Carpometacarpus (M-110, 341 M-176, 164 M-101, 724 M-558)—Table 14. Femur (517 M-179)—Table 17. Tibiotarsus (340 M-176, 759 M-176, 174 M-101, 335 M-1336)—Tables 18, 19. Tarsometatarsus (775 M-300, 170 M-101, 725 M-645, 401 M-108D, 783 M-2027)—Tables 20–22. Reported as *M. ocellata* by Wing and Steadman (in press), this series agrees with modern skeletons of *M. ocellata*.

MAYAPÁN, Yucatán, México. *Meleagris ocellata*. All are MCZ 2536–2539, 2543, 2445. Numbers in parentheses are numbers of specimens examined. Coracoid (41)—Tables 4, 5. Scapula (39)—Tables 6, 7. Humerus (31)—Tables 8, 9. Carpometacarpus (27)—Tables 14, 15. Tarsometatarsus (20)—Tables 20–22. This very large series of bones, reported as *M. ocellata* by Pollock and Ray (1957) and as *Agriocharis ocellata* by Brodkorb (1964a), includes many specimens that are larger and stouter than the corresponding elements in comparative skeletons of wild *M. ocellata*. This is strong evidence for artificial fattening of these birds, such as by feeding them corn, in combination with a sedentary existence. This in turn suggests that these birds were kept in some state of confinement by the people of Mayapán. To what extent *M. ocellata* was tamed at Mayapán is presently impossible to ascertain. *Meleagris ocellata* is famous for its wildness, and numerous references attest to the impossibility of taming this beautiful bird. However, an example of its potential to attain at least some degree of tameness has been observed by the author at Tikal National Park, Petén, Guatemala, where because of protection from hunting for about 20 years, the two local flocks of *M. ocellata* living near the ruins are so tame as to come up to homes and be fed corn and rice by the residents. These birds may easily be approached to within about 8 meters, while birds from flocks in adjacent areas, which are subjected to hunting, are extremely wary and fly or run away at first sight of a person (Steadman et al. 1979). The presence also at Mayapán of apparently wild *M. ocellata* suggests that wild birds were eaten along with those supposedly reared. The sample of wild turkeys hunted by the Maya was probably biased toward those birds that fed heavily in the corn fields and were thus in good flesh.

CANCÚN ISLAND, Quintana Roo, México. *Meleagris* cf. *M. ocellata*. Tarsometatarsus (UFZA Q-509)—Table 20. No characters apparent other than size (immature).

TULÚM, Quintana Roo, México. *Meleagris* cf. *M. ocellata*. Ulna (MCZ 2513)—Table 10. Carpometacarpus (MCZ 2531)—Table 15. These specimens lack distinctive qualitative characters, and are very tentatively referred to *M. ocellata* on the basis of their very small size.

BARTON RAMIE SITE, Belize. *Meleagris* cf. *M. ocellata*. Tarsometatarsus (PB 8492)—Table 21. No characters apparent other than size. Reported as *Agriocharis ocellata* by Brodkorb (1964a).

MACANCHÉ, Petén, Guatemala. *Meleagris* cf. *M. ocellata*. Both are UFZA unnumbered. Carpometacarpus—Table 14. Tibiotarsus—Table 18. No characters apparent other than size.

SYSTEMATICS

The nomenclatural status of the turkeys from each of the sites listed above and in Table 1 is based on data in the Comparative Osteology section (roughly quantified in Tables 2 and 3) and also on the measurements presented in Tables 4–22. As previously noted, turkeys are very similar osteologically, and most quantitative differences are only average ones. With the exception of the problematical *Rhegminornis calobates*, from which only one element is known, each taxon of turkey averages more than partial agreement (i.e., a similarity index value greater than 50) with all other known forms. Tables 2 and 3 are based only on those characters in which a difference was seen between at least two forms. The degree of similarity would be much higher if previously published characters that do not hold were included. It must be understood that biases exist in Tables 2 and 3 because of differences in elements and characters being compared between any two taxa. These tables present only an approximate, but useful, estimate of the degree of similarity between the various forms of turkeys.

Recognition of the genera *Rhegminornis* and *Proagriocharis* is based on their low overall resemblance to other forms (Tables 2–4, 20–22). A more detailed discussion of their affinities is given in the accounts of individual sites above. *Meleagris* is the only other genus recognized in this study. It includes all known diagnostic turkey fossils from Blancan through Recent times, as well as the two living species. The two other genera recognized by Brodkorb (1964a) and most other workers, *Agriocharis* and *Parapavo*, are herein regarded as synonyms of *Meleagris*, for reasons outlined as follows.

Agriocharis was originally diagnosed on the external morphology of *M. ocellata*. Chapman (1896:288) described the new genus as follows: "The differences in the form and distribution of the warty excrescences of the head and neck, and in the character of the erectile appendages of the forehead, the more highly graduate tail and the more rounded rectrices, the absence of a beard in the male and the presence of rudimentary spurs in the female are all characters which entitle *ocellata* to generic distinction. . . ." Rudimentary spurs in females, discussed earlier in the Comparative Osteology section, are not always present in females of *M. ocellata*, and they may be present in females of *M. gallopavo*. *Meleagris ocellata* is characterized by a lower average amount of similarity to other turkeys than any other post-Hemphillian form (Tables 2 and 3), being approached in this respect only by *M. crassipes*. However, *M. ocellata* resembles post-Hemphillian forms more than it does *Rhegminornis calobates* or *Proagriocharis kimballensis*, and the rather low level of agreement between *M. ocellata* and *M. gallopavo* is skewed downward because complete skeletons of these living species permitted me to find characters that were imperceptible in fossil forms. In Table 2, *M. ocellata* and *M. gallopavo* are compared in 85 different characters, ten more than are used between any other forms. All of these ten characters have a similarity value of 0 to 50. Regardless, the amount of dissimilarity between the various Pleistocene and Recent forms and *M. ocellata* is not enough to justify generic separation. Although both *M. ocellata* and *M. crassipes* appear to be somewhat unique within the genus, I feel that the similarities between these species, which in the past have been largely overlooked in a search for differences, may best be emphasized by their inclusion in a single genus. Ridgway (Ridgway and Friedmann 1946:458) recognized *Agriocharis* but said, "*Agriocharis* is, in fact, so closely related to *Meleagris* that I am somewhat doubtful as to the expediency of recognizing it as a genus." Paynter (1955) found the characters of *M. ocellata* to be of no more than specific value after several years of field and museum work with the birds of the Yucatán peninsula. Nearly two months of observation of *M. ocellata* at Tikal, Guatemala, has revealed many similarities between the life histories of *M. ocellata* and *M. gallopavo* (Steadman et al. 1979). Thus, non-osteological data exist that support the inclusion of *Agriocharis* in *Meleagris*.

Meleagris californica is more similar to *M. gallopavo* than to *M. ocellata* (Tables 2 and 3), and is consistently intermediate between the two living species in size (Tables 4–22). L. Miller (1916a) said that because *M. californica* was intermediate between *M. ocellata* and *Pavo cristatus*, species that are in different subfamilies, it was necessary to erect the genus *Parapavo* for that species. Howard (1927) correctly regarded *M. californica* as distinctly meleagridine, not phasianine. Howard (1927) considered *M. (Parapavo) californica* to be generically separable from *M. gallopavo* and *M. ocellata*, although resembling *M. ocellata* more than *M. gallopavo*, and stated (1927:27): "Grouping the characters for each element together, we find that the following elements [of *M. californica*] possess characters of each of the modern genera: sternum, coracoid, humerus, radius, femur, tibiotarsus, tarsometatarsus; another element (furcula) is in all characters nearer *Meleagris* [*gallopavo*]; others in all characters approach *Agriocharis* [*ocellata*]: skull, scapula, ulna. The remaining elements either possess characters distinct from both genera (fibula), or have structure features common to all three genera (carpometacarpus, pelvis, pygostyle)." Thus, *M. californica* was supposedly distinct from both *M. gallopavo* and *M. ocellata* only in the fibula. However, the fibula of these species is not as definitely different as stated by Howard (see page 137). The lack of diagnostic features in *M. californica*, especially as compared to *M. gallopavo*, strongly argues for its inclusion in *Meleagris*. A. Miller and Bowman (1956) found no generic differences between the tarsometatarsi of *Meleagris* (*gallopavo*) and *Parapavo* (*californica*). I concur with this and add that I cannot find generic differences between *M. californica* and *M. gallopavo* in any skeletal element.

The general recognition of the genus *Parapavo* for the past 60 years can perhaps be attributed largely to two factors. First, it was originally described as a peacock in the genus *Pavo* (L. Miller 1909); when its true subfamilial affinities became apparent (L. Miller 1916a), to synonymize *Pavo* with a living genus of turkey probably seemed to be a bit drastic, if indeed it was even considered. Second, throughout the subsequent systematic history of *M. californica* (Howard 1927, 1928; Sushkin 1928), the two living species of turkeys were placed in separate genera. Thus comparisons among *M. californica*, *M. gallopavo*, and *M. ocellata* were carried out with a bias toward thinking in terms of differences on the generic level (*Parapavo* vs. *Meleagris* vs. *Agriocharis*). I have shown above that the majority of those differences either do not hold at all, or are only average differences that must therefore be considered on a specific, not a generic, level.

REVISED CLASSIFICATION

Order Galliformes (Temminck 1820)

Family Phasianidae Vigors 1825

Subfamily Meleagridinae (Gray 1840)

Rhegminornithidae Wetmore 1943 (23 June), Proc. New England Zool. Club, vol. 22, p. 60 (type *Rhegminornis* Wetmore).—Rhegminornithinae Brodkorb 1967 (12 June), Bull. Florida State Mus., Vol. 11, no. 3, p. 201 (new rank).

Genus *Rhegminornis* Wetmore 1943

Rhegminornis Wetmore 1943 (type *Rhegminornis calobates* Wetmore)

Rhegminornis calobates Wetmore 1943

Rhegminornis calobates Wetmore 1943 (23 June), Proc. New England Zool. Club, vol. 22, p. 61, pl. 9, figs. 1–5 (type from Thomas Farm, distal end of right tarsometatarsus, Mus. Comp. Zool. no. 2331).—*Rhegminornis calobates,* Olson and Farrand 1974 (June), Wilson Bull., vol. 86, no. 2, p. 114 (reassignment from Charadriiformes to Meleagridinae).

Early Miocene (Hemingfordian): Thomas Farm local fauna. Florida: Gilchrist County: Thomas Farm, 8 miles N of Bell.

Genus *Proagriocharis* Martin and Tate 1970

Proagriocharis Martin and Tate 1970 (type *Proagriocharis kimballensis* Martin and Tate)

Proagriocharis kimballensis Martin and Tate 1970

Proagriocharis kimballensis Martin and Tate 1970 (5 June), Wilson Bull., vol. 82, no. 2, p. 215, fig. 1 (type from S of Lime Creek, left coracoid, Univ. Nebraska State Mus. no. 20033).

Late Miocene or early Pliocene (Hemphillian): lower part of Kimball Formation, Univ. Nebraska Coll. Loc. Ft-40. Nebraska: Frontier County: S of Lime Creek.

Genus *Meleagris* Linnaeus 1758

Meleagris Linnaeus 1758 (type *Meleagris gallopavo* Linnaeus)
Agriocharis Chapman 1896 (type *Meleagris ocellata* Cuvier)
Eumeleagris Coues 1903 (type *Meleagris ocellata* Cuvier)
Meleagrops (Marsh ms.) Shufeldt 1913 (type *Meleagris celer* Marsh)
Parapavo L. Miller 1916a (type *Pavo californicus* L. Miller)

Meleagris progenes (Brodkorb 1964)

Meleagris gallopavo; Meleagrididae, sp.?, Wetmore 1944. Univ. Kansas Sci. Bull., vol. 30, pt. 1, no. 9, p. 98 (Rexroad ranch, misidentification).

Agriocharis progenes Brodkorb 1964b (4 Nov.), Quart. Jour. Florida Acad. Sci., vol. 27, no. 3, p. 223, pl. 1, figs. 1–3 (type from Rexroad ranch, distal part of right tarsometatarsus, Univ. Michigan Mus. Paleo. no. 31034).

Late Pliocene (Blancan): Rexroad Formation, Rexroad local fauna. Kansas: Meade County: Rexroad ranch, locality 3.

Meleagris leopoldi
A. Miller and Bowman 1956

Parapavo californicus, L. Miller and Johnston 1937, Condor, vol. 39, no. 5, p. 229 (Cita Canyon, misidentification).

cf. *Meleagris,* Johnston and Savage 1955, Univ. California Publ., Geol. Sci., vol. 31, no. 2, p. 39.

Meleagris leopoldi A. Miller and Bowman 1956 (5 March), Wilson Bull., vol. 68, no. 1, p. 42, figs. 1a–1c (type from Newton Harrell-Edd Reynolds ranch, distal end of right tarsometatarsus, Panhandle Plains Hist. Mus. no. 753)—*Agriocharis leopoldi,* Brodkorb 1964a (26 June), Bull. Florida State Mus., vol. 8, no. 3, p. 324.—Brodkorb 1964b (4 Nov.), Quart. Jour. Florida Acad. Sci., vol. 27, no. 3, p. 225.

Late Pliocene (Blancan): Cita Canyon beds. Texas: Randall County: Cita Canyon local fauna, UCMP locality V-3721, at Newton Harrell-Edd Reynolds ranch, 2.2 km S and 21 km E of Canyon.

Meleagris anza (Howard 1963)

Agriocharis anza Howard 1963 (30 Dec.), Los Angeles County Mus., Contr. in Sci., no. 73, p. 19, pl. 3, fig. A (type from Arroyo Tapiado, right humerus, Los Angeles County Mus. no. 3753).

Early Pleistocene (Irvingtonian): upper Palm Spring Formation, upper 4000 ft. of Vallecito-Fish Creek section, Nat. Hist. Mus. Los Angeles County Loc. no. 1358. California: San Diego County: Anza-Borrego State Park: Arroyo Tapiado.

Meleagris gallopavo Linnaeus 1758

Meleagris gallopavo Linnaeus 1758, Systema Naturae, ed. 10, vol. 1, p. 156 (type from México).

Meleagris altus Marsh 1870a (March), Proc. Acad. Nat. Sci. Philadelphia, p. 11 (nomen nudum).—Marsh 1870b (July), Amer. Naturalist, vol. 4, no. 5, p. 317 (type from Manalapan, New Jersey, portions of 3 skeletons).—Marsh 1872 (October), Amer. Jour. Sci., ser. 3, vol. 4, no. 22, p. 260 (descr. humerus, coracoid, femur, tibia, tarsometatarsus).—Mercer 1899, Jour. Acad. Nat. Sci. Philadelphia, ser. 2, vol. 11, pt. 2, p. 280 (referred tarsometatarsus from Port Kennedy Cave, Pennsylvania).

Meleagris superbus Cope 1871, Trans. Amer. Philos. Soc., n.s., vol. 14, pt. 1, p. 238 (types from Manalapan, New Jersey, 2 tibiae, 2 femora, 1 coracoid).—Peterson 1926, Ann. Carnegie Mus., vol. 16, no. 2, p. 254, pl. 17, figs. 1–10 (referred 1 scapula, 1 humerus, 1 pelvis, 2 femora, 2 tibiotarsi, 2 tarsometatarsi from Frankstown Cave, Pennsylvania).—*Meleagris superba,* Shufeldt 1915, Trans. Connecticut Acad. Arts Sci., vol. 19, p. 66, pl. 10, figs. 71—73; pl. 11, figs. 74–77 (Marsh's types from Manalapan, 3 humeri, 1 radius, 1 ulna, 1 coracoid, 1 scapula, 2 femora, 2 tibiotarsi, 1 tarsometatarsus, Yale Peabody Mus. nos. 533–536); *M. altus* considered a synonym.

Meleagris celer Marsh 1872 (October), Amer. Jour. Sci., ser. 3, vol. 4, no. 22, p. 261 (types from Manalapan, New Jersey, tibiotarsus and tarsometatarsus). *Meleagrops celer* (Marsh ms.), *Meleagris celer.*—Shufeldt 1913, Auk, vol. 30, no. 1, p. 29, pl. 3, figs. 3–5 (Marsh's type tarsometatarsus from Manalapan, Yale Peabody Mus.).

Ardea sellardsi Shufeldt 1917, Florida Geol. Surv., Ninth Annual Rept., p. 38, pl. 2, fig. 15 (type tibiotarsus from Vero Beach, Florida).—*Meleagris gallopavo,* Wetmore 1931a, Smithsonian Misc. Coll., vol. 85, no. 2, p. 33 (Shufeldt's type from Vero Beach, formerly Florida Geol. Surv. no. 7551, now in U.S. Nat. Mus.).

Meleagris tridens Wetmore 1931a (13 Apr.), Smithsonian Misc. Coll., vol. 85, no. 2, p. 33, fig. 13, pl. 6 (type from Seminole Field, Florida, tarsometatarsus, U.S. Nat. Mus. no. 12052).

Late Pleistocene (Rancholabrean) through Holocene: eastern, central, and southwestern United States, and parts of eastern and western México.

Meleagris californica (L. Miller 1909)

Pavo californicus L. Miller 1909 (14 Aug.), Univ. Calif. Publ., Bull. Dept. Geol., vol. 5, no. 19, p. 285, pl. 25 (type from Rancho La Brea, right tarsometatarsus, Univ. Calif. Mus. Paleo. no. 11300).—*Parapavo californicus,* L. Miller 1916a (10 March), Univ. Calif. Publ., Bull. Dept. Geol., vol. 9, no. 7, p. 96.

Meleagris richmondi Shufeldt 1915 (Feb.), Trans. Connecticut Acad. Arts Sci., vol. 19, p. 67, pl. 2, fig. 19 (type from Mission San Jose, California, fragmentary sternum, Yale Peabody Mus. no. 905).—*Parapavo californicus,* Brodkorb 1964a (26 June), Bull. Florida State Mus., vol. 8, no. 3, p. 326.

Late Pleistocene (Rancholabrean): asphalt pits, Rancho La Brea local fauna. California: Los Angeles County, Rancho La Brea (L. Miller 1909).

Meleagris ocellata Cuvier 1820

Meleagris ocellata Cuvier 1820, Mem. Mus. Hist. Nat., vol. 5, no. 1, p. 4, pl. 1 (type from Gulf of Honduras).—*Agriocharis ocellata,* Chapman 1896, Bull. Amer. Mus. Nat. Hist., vol. 8, p. 287.—*Eumeleagris ocellata,* Coues 1903, Key to North Amer. Birds, vol. 2, ed. 5, p. 727.

Holocene: Belize, northern Guatemala, eastern Chiapas, and eastern Tabasco through Campeche, Yucatán, and Quintana Roo, México.

Meleagris crassipes L. Miller 1940

Meleagris crassipes L. Miller 1940 (15 May), Condor, vol. 42, no. 3, p. 154, figs. 44–45 (type from San Josecito Cavern, tarsometatarsus, Calif. Inst. Techn. no. 2708, now in Nat. Hist. Mus. Los Angeles County).—*Agriocharis crassipes,* Brodkorb 1964b (4 Nov.), Quart. Jour. Florida Acad. Sci., vol. 27, no. 3, p. 225.

Late Pleistocene (Rancholabrean): cave deposit, San Josecito Cave local fauna. México: Nuevo León: San Josecito Cave, near Aramberri.

EVOLUTION

Rhegminornis calobates is morphologically unique among the species included in this study (Tables 3, 21). Its relationships to younger species are poorly understood, although there is a suggestion of relatively close affinities to *Proagriocharis kimballensis* (Table 3). The somewhat younger (Clarendonian?) tibiotarsus from Westmoreland Park, Virginia, is much too large for *R. calobates* and is also larger than *P. kimballensis*. Typically for a tibiotarsus, this specimen suffers a lack of diagnostic characters that prevents further elucidation of its place in meleagridine phylogeny.

The relationships of *Proagriocharis kimballensis* to any of the younger turkeys are also quite uncertain. If a trend of increasing size with decreasing age occurred in late Hemphillian and early Blancan times, as it did from the late Blancan through the Rancholabrean in the *M. gallopavo* lineage, *P. kimballensis* could qualify as a possible ancestor of *M. progenes* on the basis of its size and age. But the low similarity between these two species (Table 2), although probably due at least in part to the sample sizes involved, does not give strong support for such a lineage. Sadly, other Hemphillian turkey fossils, all larger than *P. kimballensis,* are represented only by tibiotarsi from Bone Valley, Florida, and Buckhorn, New Mexico. These previously unreported fossils, both of which are tentatively referred to *Meleagris,* and the Upper Miocene (Clarendonian?) tibiotarsus from Virginia, suggest that *Proagriocharis* and perhaps *Rhegminornis* represent a sibling group of the larger main line of turkeys.

Meleagris progenes is most similar to *M. leopoldi* and fossils from Inglis and Coleman (Table 2), suggesting that only one lineage is represented by these four populations, with *M. leopoldi* intermediate, both morphologically and temporally, between *M. progenes* and the Inglis-Coleman forms.

The turkeys from Inglis and Coleman are very closely related and certainly represent only one lineage. The qualitative characters of the Vallecito Creek specimen (*M. anza*) are within the range of variation of Inglis specimens. All humeral characters that supposedly distinguish the Vallecito Creek turkey from Inglis turkeys are either definitely or quite possibly due to the crushing of the Vallecito Creek fossil, hence the tentative referral of the Inglis specimens to this species. Extending the range of a species of fossil turkey from California to Florida is not unreasonable in light of the present distribution and varied choice of habitat of *M. gallopavo.* The paleoecological evidence (Downs and White 1968; Hibbard 1970; Hibbard and Dalquest 1966; Howard 1963; Klein 1971; Martin 1974) suggests fairly similar habitats for these Irvingtonian sites, further increasing the likelihood of a single, wide-ranging species or an osteologically similar superspecies of turkey existing during the early and middle Irvingtonian. In this regard, however, I must say that turkeys are very limited in their utility as paleoecological indicators. Aside from needing trees in which to roost, it is quite difficult to generalize about the habitat of *M. gallopavo,* discussions of which are found in Hewitt (1967), Leopold (1948), and Schorger (1966); see also Leopold (1948), and Steadman et al. (1979), for habitat requirements of *M. ocellata.* The use of *M.* ("*Agriocharis*") *anza* by Hibbard and Dalquest (1966) to suggest environmental conditions in the early Pleistocene of north-central Texas as being perhaps similar to those of the modern Yucatán peninsula is particularly inappropriate, not only because of the above mentioned vagueness in the definition of turkey habitat, but also because the femur from Gilliland, Texas, which Brodkorb (1964b) referred to *M.* ("*Agriocharis*") *anza,* is not even safely identifiable to genus (see discussion of Gilliland in Systematics section).

No turkey fossils older than Rancholabrean are even tentatively referable to *M. gallopavo,* although the Colemen specimens, when compared to earlier forms, are definitely approaching the *M. gallopavo* grade and are clearly intermediate between specimens from Inglis and *M. gallopavo.* There is little doubt that *M. gallopavo* evolved from the Coleman-type turkey. How much of the present range of *M. gallopavo* was occupied by this form in late Irvingtonian times is not known. Perhaps the *M. gallopavo* grade was attained initially in only a small portion of this present range. This contradicts the following statement of Hibbard and Dalquest (1966:14), "It appears that these southern members [*M. progenes, M. leopoldi,* and *M. anza*; at the time thought to be more closely related to *M. ocellata* than to *M. gallopavo*] were slowly displaced southward by the progressively cooler climates produced by each successive glaciation. The more northern turkey, *Meleagris gallopavo,* was able to extend its range southward with the development of the strong continentality of the climate during Wisconsin time." This statement implies that the earlier forms ("southern members") were dead-end taxa that existed contemporaneously with *M. gallopavo.* It is a basic thesis of my studies, however, that these Blancan and Irvingtonian turkeys are not drastically different from the living *M. gallopavo* and, in fact, probably represent its direct ancestors.

Holman (1964) noted that the pneumatic foramen on the dorsal base of the shaft of the scapula distinguishes living Meleagridinae from other gallinaceous birds. As noted in the Comparative Osteology section, *Meleagris progenes* of Rexroad (Blancan) and *Meleagris* cf. *M. leopoldi* or *M. anza* from Inglis IA (earliest Irvingtonian) lack this foramen, which is present in the late Irvingtonian species of *Meleagris* from Haile XVIA and Coleman IIA, as well as *M. californica* (Rancholabrean), and the living *M. gallopavo* and *M. ocellata.* All species of Phasianinae that I have examined lack this foramen except *Pavo cristatus* and *P. muticus.* Increased pneumaticity of the scapula may be related to increased size, as *Pavo* and *M. gallopavo* are the largest phasianines and meleagridines, respectively, and *Meleagris* sp. of Coleman is larger than *M. progenes* or the Inglis specimens. The foramen in *Pavo* is between the glenoid facet and the furcular articulation, but, in meleagridines, the foramen lies more posteriorly on the base of the shaft, away from articulating surfaces. This difference in position, combined with documentation from fossils from Rexroad, Inglis, Haile XVIA, and Coleman on the development of this foramen during Irvingtonian times, and the lack of a foramen in all Phasianinae but *Pavo,* suggests that a non-foraminate scapula is the primitive condition in both the Phasianinae and Meleagridinae, and the foraminate scapula is the derived state. The presence of a pneumatic foramen in *M. gallopavo, M. ocellata,* and *M. californica* thus strongly argues for their common ancestry in the middle Irvingtonian. Both *M. ocellata* and *M. californica* are smaller than Inglis specimens. If they branched off from the Inglis-Coleman lineage before reaching the foraminate condition, the foramen may not have been expected to evolve in these species. Therefore, *M. gallopavo, M. ocellata* and *M. californica* are probably derived from isolated populations of a Coleman-like turkey, after the development of the foraminate scapula. This is further supported by these three forms each being more similar to specimens from Coleman than to those from Inglis (Table 2). The ancestors of *M. californica* and *M. ocellata* in the late Irvingtonian were not necessarily identical to the Coleman turkey, because as much variation probably occurred in this widespread species or superspecies as occurs in *M. gallopavo* today (compare tarsometatarsal measurements and ratios of *M. g. silvestris* and *M. g. osceola* in Tables 20 and 22).

Meleagris ocellata, which has no fossil record in the Pleistocene, may have evolved from a population of turkeys similar to those of Coleman that became isolated in the Yucatán region by a high stand of the sea during an interglacial period in middle to late Irvingtonian times. No turkeys live today in the very wet coastal lowlands of western Tabasco to central Veracruz, México. Thus it appears that this wet tropical forest forms a barrier between present populations of *M. ocellata* in the Yucatán region and *M. gallopavo intermedia* in coastal northern Veracruz and Tamaulipas. This barrier probably did not exist continuously in the Pleistocene, as documented by Martin (1974), who found strong western and neotropical affinities in the Coleman mammals, many of which probably entered Florida via a Gulf Coast savanna corridor. This implies somewhat more xeric conditions than at present, increasing the likelihood that turkeys were living in even the wettest portions of the Gulf Coast. Thus, it is likely that the Coleman-type turkey occurred around the entire Gulf Coast area when the "savanna corridor" existed. The distance involved would not be great, as a drop in sea level of 100 meters during a glacial period would have decreased the land distance from Tampa, Florida, to Mérida, Yucatán, from about 3600 to about 2400 kilometers (Webb 1974).

Meleagris californica undoubtedly evolved from populations that became isolated in California, where turkeys are known to occur as early as the Hemphillian or Blancan (University Drive site). The high degree of similarity between *M. californica* and *M. gallopavo* suggests either that these two species were subject to fairly similar selective forces after populations of their common ancestors became isolated, or that the ancestors of *M. californica* became isolated in California only after reaching the *M. gallopavo* grade. *Meleagris gallopavo* is not known west of central Arizona today. The quite arid conditions in western Arizona and southeastern California that prevail today could easily have provided a barrier to gene flow between the turkeys of southwestern California and southeastern Arizona.

The relationships of *M. crassipes* to other turkeys is difficult to assess at this point. It is the smallest of the various species of *Meleagris* and is perhaps best characterized by its rather distinctive tarsometatarsus. It resembles *M. californica* more than other congeners (Tables 2 and 3), but it also has a fair degree of qualitative and quantitative similarity to *M. progenes,* a form known only from Kansas and Arizona. A more complete discussion of *M. crassipes* is found in Amadeo Rea's paper in this volume.

The idea of a phasianine origin of the Meleagridinae is supported by the phasianine nature of the furcula (characters 3, 5, 9), scapula (character 3), and tarsometatarsus (characters 4, 6, 7) in the first meleagridines in which these elements are known, as well as general osteological similarity. Therefore, I propose that turkeys originated from a phasianine stock that either (1) became isolated in the New World and evolved *in situ* or (2) invaded the New World after reaching the meleagridine grade in the Old World. The presence of the above mentioned phasianine characters in various turkeys favors the first hypothesis, as does the lack of recognized meleagridine fossils in the Old World. If one considers turkeys as having come to North America via a land corridor over the Bering Strait, then they would have dispersed through North America from west to east, rather than vice versa. Details of this dispersal cannot be presently defined. However, the apparent turkey from the late Miocene of Virginia and *Rhegminornis* from the early Miocene of Florida suggest the potential for Miocene and perhaps earlier turkey-like fossils from central and western North America. A plausible alternative to the Bering Strait dispersal route is that of an early Tertiary route from western Europe to eastern North America. Available fossil evidence favors neither hypothesis.

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AMNH	American Museum of Natural History (Charlotte Holton, Malcolm McKenna).
ANSP	Academy of Natural Sciences of Philadelphia (David Gillette, Storrs Olson).
CM	Carnegie Museum of Natural History (John Guilday, Mary Dawson, Wendy Pollock, Mary Clench, Kenneth Parkes, Miriam Stern).

F:AM	Frick Collection, American Museum of Natural History (Malcolm McKenna).
GW	Glen Woolfenden.
ISUM	Idaho State University Museum (H. Gregory McDonald, John White).
LACM	Natural History Museum of Los Angeles County (Robert McKenzie, David Whistler).
MCZ	Museum of Comparative Zoology, Harvard University (Raymond Paynter).
PB	Pierce Brodkorb.
PPHM	Panhandle Plains Historical Museum (James Hanson, Gerald Schultz, Jackie Wilson).
PU	Princeton University, Museum of Natural History (Donald Baird).
SBU	Saint Bonaventure University, Department of Biology (Stephen Eaton).
TMM	Texas Memorial Museum, University of Texas (Janette Bannan, Ernest Lundelius).
TTU	Texas Tech University.
UCMP	University of California, Berkeley, Museum of Paleontology (J. Howard Hutchison).
UCMVZ	University of California, Berkeley, Museum of Vertebrate Zoology (Ned Johnson, Victoria Dziadosz, National Science Foundation Grant BMS 2700102).
UF	University of Florida, Florida State Museum (S. David Webb, Chandra Aulsbrook).
UFZA	University of Florida, Florida State Museum Zooarchaeological Collection (Elizabeth S. Wing).
UK	University of Kansas, Museum of Natural History (Marion Mengel).
UMMP	University of Michigan, Museum of Paleontology (Claude Hibbard).
UNSM	University of Nebraska State Museum (C. Bertrand Schultz).
USNM	United States National Museum of Natural History (John Barber, Storrs Olson, Robert Purdy, Clayton Ray).
WWR	Welder Wildlife Refuge (W. Caleb Glazener).
YPM	Yale University, Peabody Museum.

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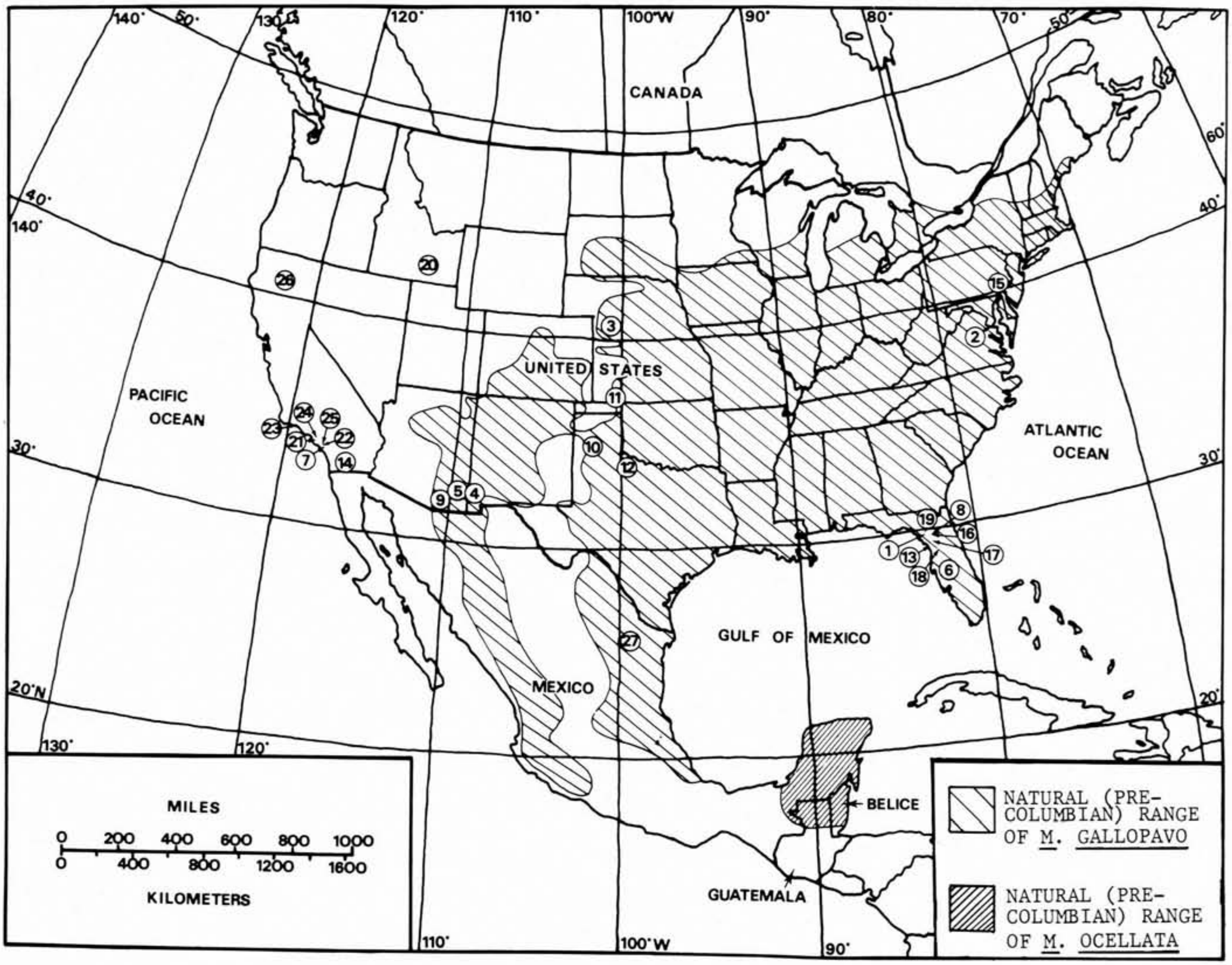

Figure 1. Distribution of fossil and living turkeys, omitting late Pleistocene (Rancholabrean) and Holocene records of *Meleagris gallopavo* and *M. ocellata* within their modern range. Numbers correspond with those in Table 1. Only sites from which specimens have been examined by the author are listed. See Rea (this vol.) for distribution of *M. crassipes*.

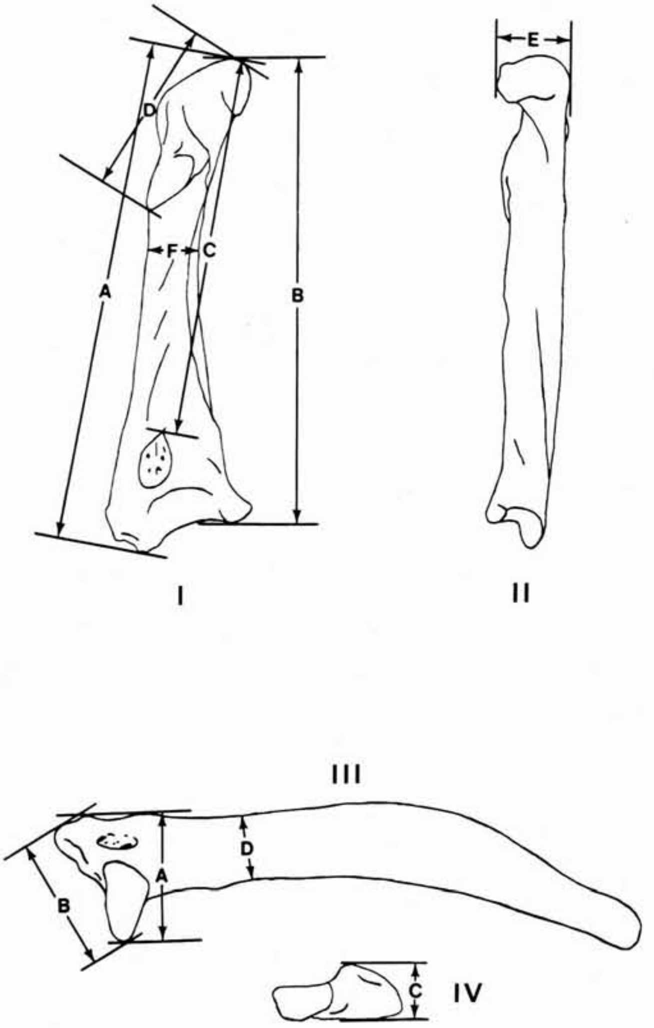

Figure 2. Measurements of the coracoid and scapula. I. Left coracoid, dorsal view: A—Head to external end of sternal facet; B—Head to internal distal angle; C—Head to pneumatic foramen; D—Head through scapular facet; F—Least width of shaft. II. Left coracoid, medial view: E—Depth of head. III. Left scapula, dorsal view: A—Proximal width; B—Tip of acromion to external tip of glenoid facet; D—Least width of neck. IV. Left scapula, proximal view: C—Depth of glenoid facet.

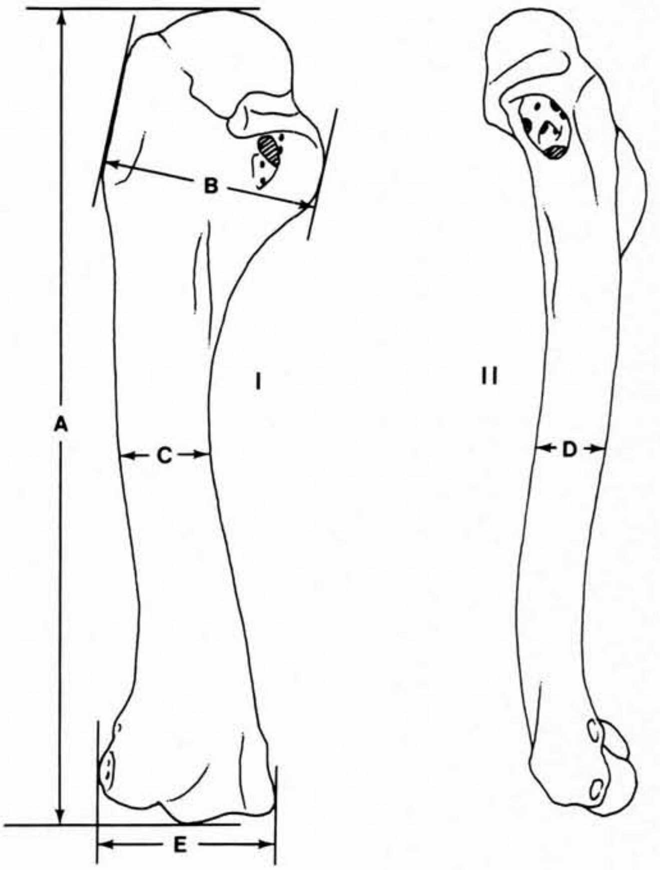

Figure 3. Measurements of the humerus. I. Left humerus, anconal view: A—Total length; B—Proximal width; C—Width of midshaft; E—Distal width. II. Left humerus, ventral view: D—Depth of midshaft.

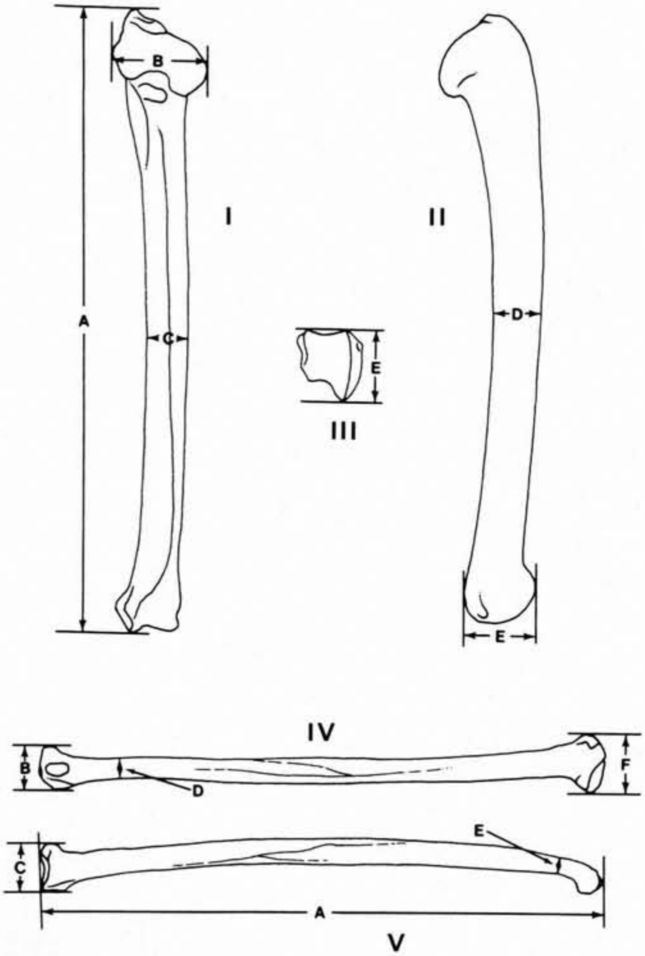

Figure 4. Measurements of the ulna and radius. I. Left ulna, palmar view: A—Total length; B—Proximal width; C—Width of midshaft. II. Left ulna, anconal view: D—Depth of midshaft; E—Distal depth. III. Left ulna, distal view: E—Distal depth. IV. Left radius, palmar view: B—Proximal width; D—Least width of shaft; F—Distal width. V. Left radius, medial view: A—Total length; C—Proximal depth; E—Least depth of shaft.

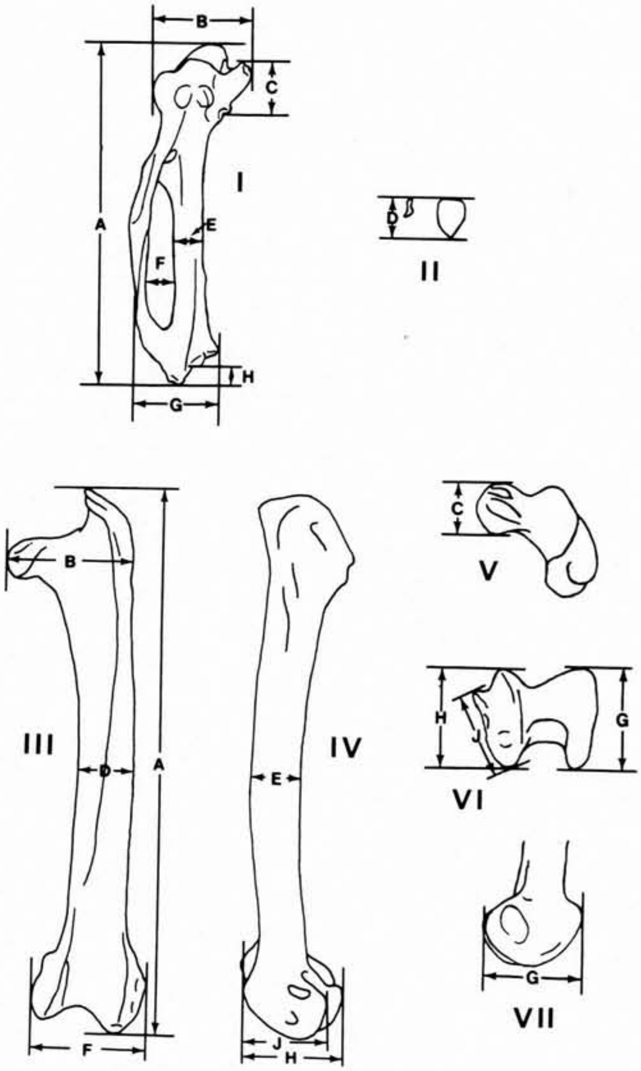

Figure 5. Measurements of the carpometacarpus and femur. I. Left carpometacarpus, internal view: A—Total length; B—Proximal depth; C—Length of metacarpal I; E—Least depth of metacarpal II; G—Distal depth; H—Protrusion of M III beyond knob of M II. II. Left carpometacarpus, cross section near center of metacarpal II: D—Least width of metacarpal II. III. Left femur, anterior view: A—Total length; B—Proximal width; D—Width of midshaft; F—Distal width. IV. Left femur, lateral view: E—Depth of midshaft; H—Depth of external condyle; J—Depth of fibular condyle. V. Left femur, proximal view: C—Depth of head. VI. Left femur, distal view: G—Depth of internal condyle; H—Depth of external condyle; J—Depth of fibular condyle. VII. Left femur, medial view: G—Depth of internal condyle.

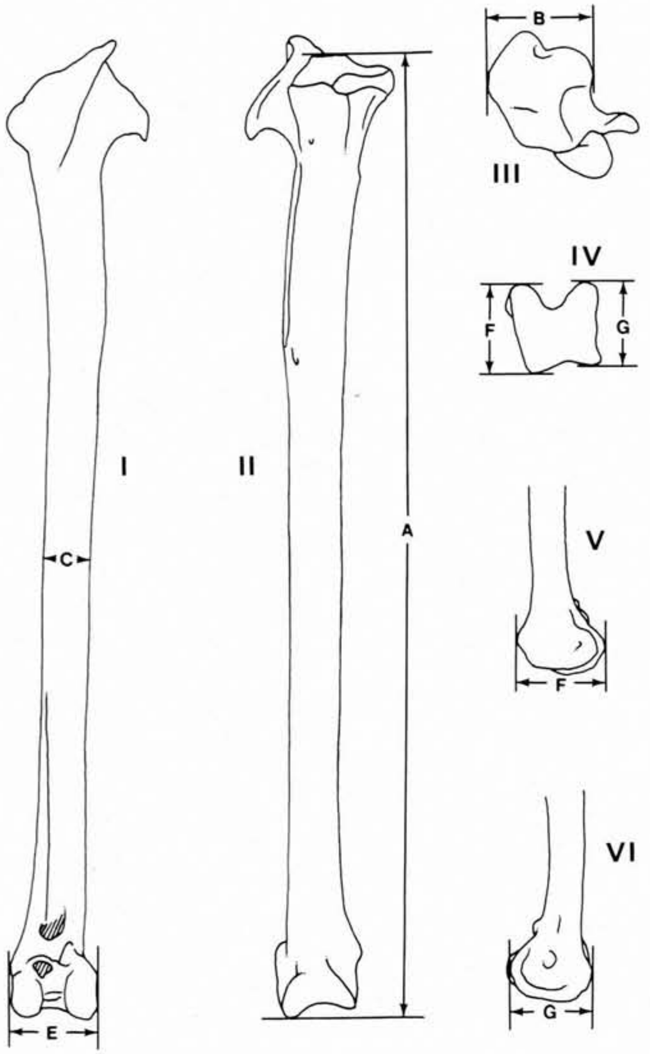

Figure 6. Measurements of the tibiotarsus. I. Left tibiotarsus, anterior view: C—Width of midshaft; E—Distal width. II. Left tibiotarsus, posterior view: A—Length without cnemial crest. III. Left tibiotarsus, proximal view; B—Width of head. IV. Left tibiotarsus, distal view: F—Depth of internal condyle; G—Depth of external condyle. V. Left tibiotarsus, medial view: F—Depth of internal condyle. VI. Left tibiotarsus, lateral view: G—Depth of external condyle.

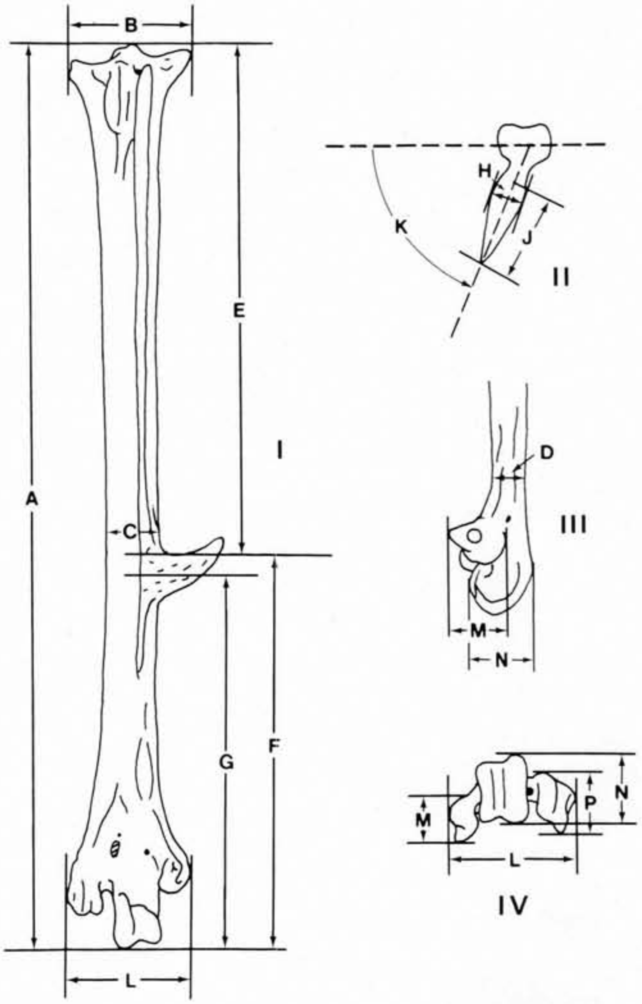

Figure 7. Measurements of the tarsometatarsus. I. Left tarsometatarsus, posterior view: A—Total length; B—Proximal width; C—Least width of shaft; E—Proximal end to middle of spur core; F—Top of spur core to end of middle trochlea; G—Middle of spur core to end of middle trochlea; L—Distal width. II. Right tarsometatarsus, cross section through spur core: H—Width of spur core; J—Length of spur core; K—Angle of spur core. III. Left tarsometatarsus, medial view: D—Least depth of shaft; M—Depth of inner trochlea; N—Depth of middle trochlea. IV. Left tarsometatarsus, distal view: L—Distal width; M—Depth of inner trochlea; N—Depth of middle trochlea; P—Depth of outer trochlea.

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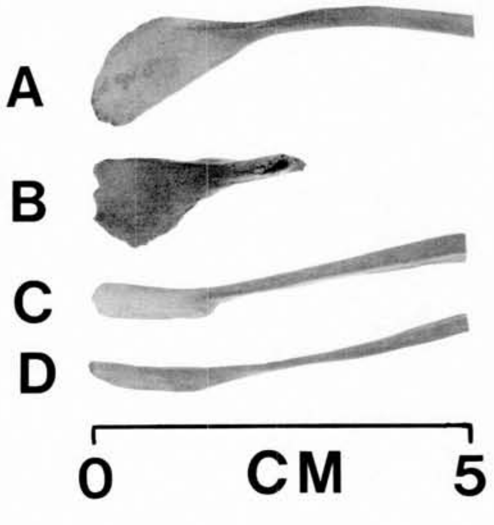
Figure 8. Lateral views of furculae of males: A. *Pavo muticus* (PB 19183); B. *Meleagris* cf. *M. leopoldi* or *M. anza* (Inglis IA; UF 20117); C. *Meleagris ocellata* (PB 23542); D. *Meleagris gallopavo osceola* (PB 27938).



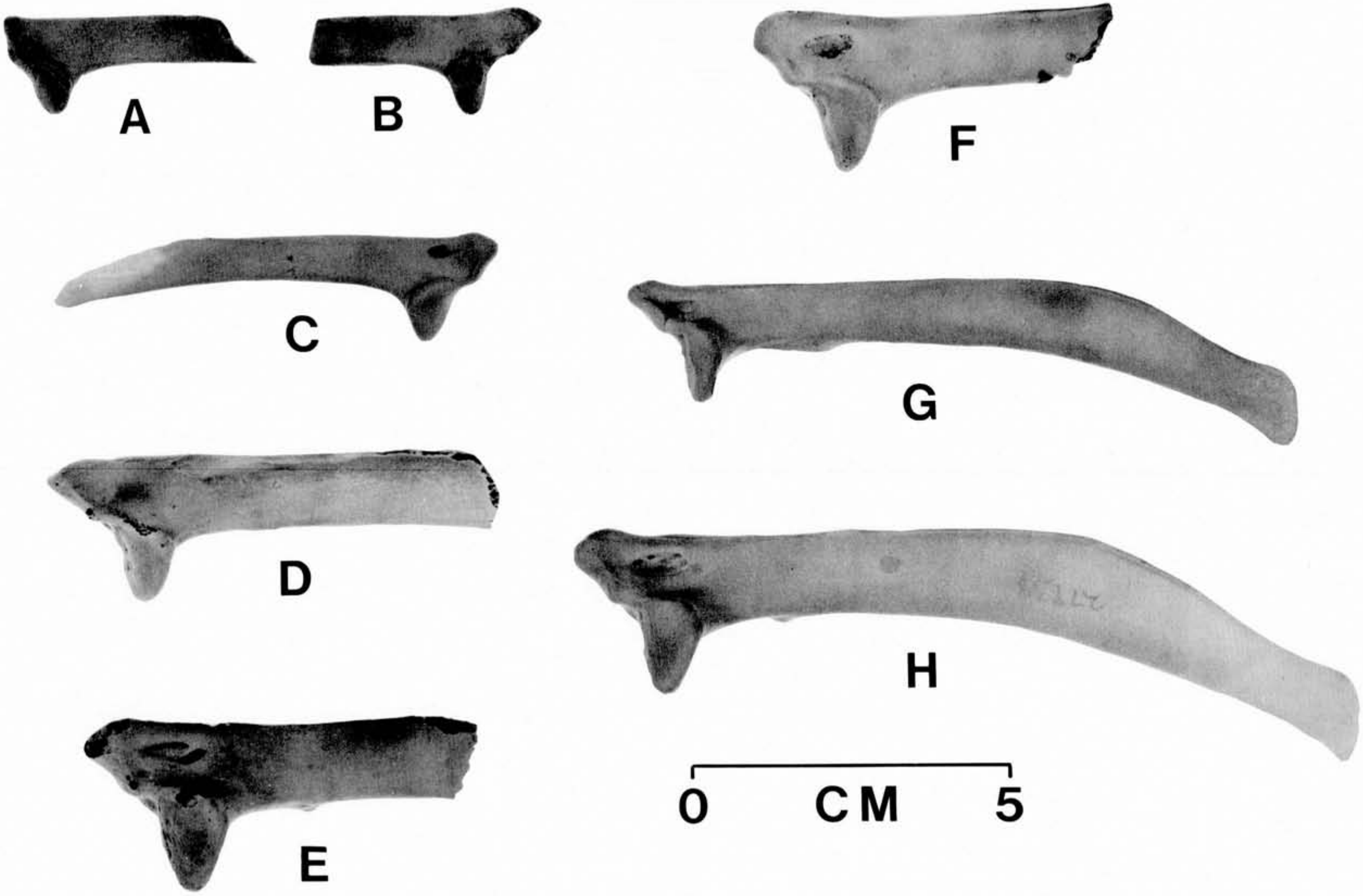


Figure 9. Dorsal views of scapulae of males: A. *Meleagris progenes* immature (Rexroad; UMMP 45965); B. *Meleagris* cf. *M. leopoldi* or *M. anza* immature (Inglis IA; UF 20208); C. *Meleagris gallopavo osceola* immature (PB 33763); D. *Meleagris* cf. *M. leopoldi* or *M. anza* adult (Inglis IA; UF 20196); E. *Meleagris* sp. adult (Coleman IIA; UF 11603C); F. *Meleagris californica* adult (Rancho La Brea; LACM E-7346); G. *Meleagris ocellata* adult (PB 23542); H. *Meleagris gallopavo osceola* adult (PB 27938).

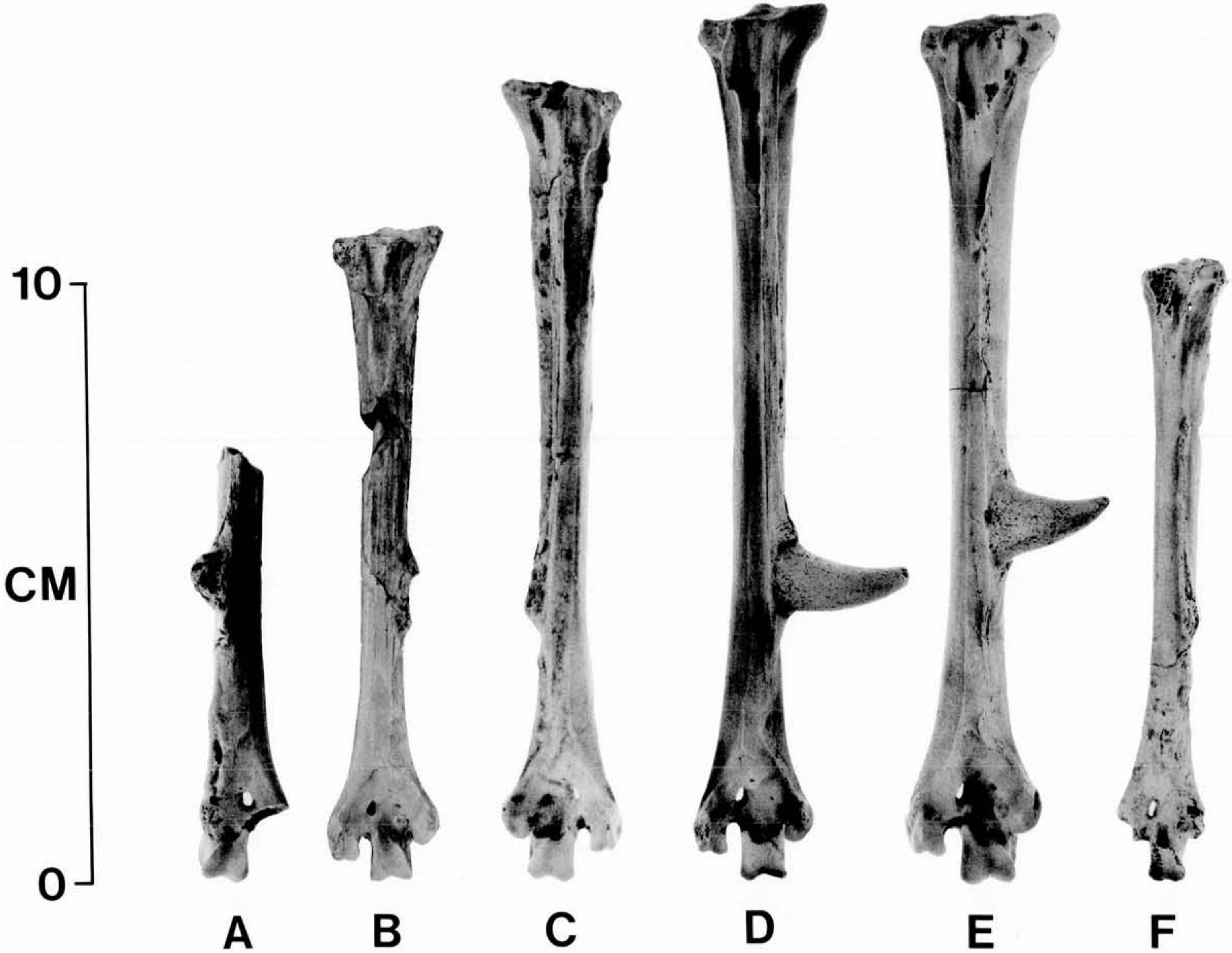


Figure 10. Posterior views of tarsometatarsi of males: A, B. *Meleagris* cf. *M. progenes* (Benson; USNM 10551, AMNH 6330); C. *Meleagris leopoldi* (Cita Canyon; PPHM 3169); D. *Meleagris* cf. *M. leopoldi* or *M. anza* (Inglis IA; UF 20713); E. *Meleagris* sp. (Coleman IIA; UF 11601N); F. *Meleagris crassipes* (San Josecito Cave; LACM UC-100023).

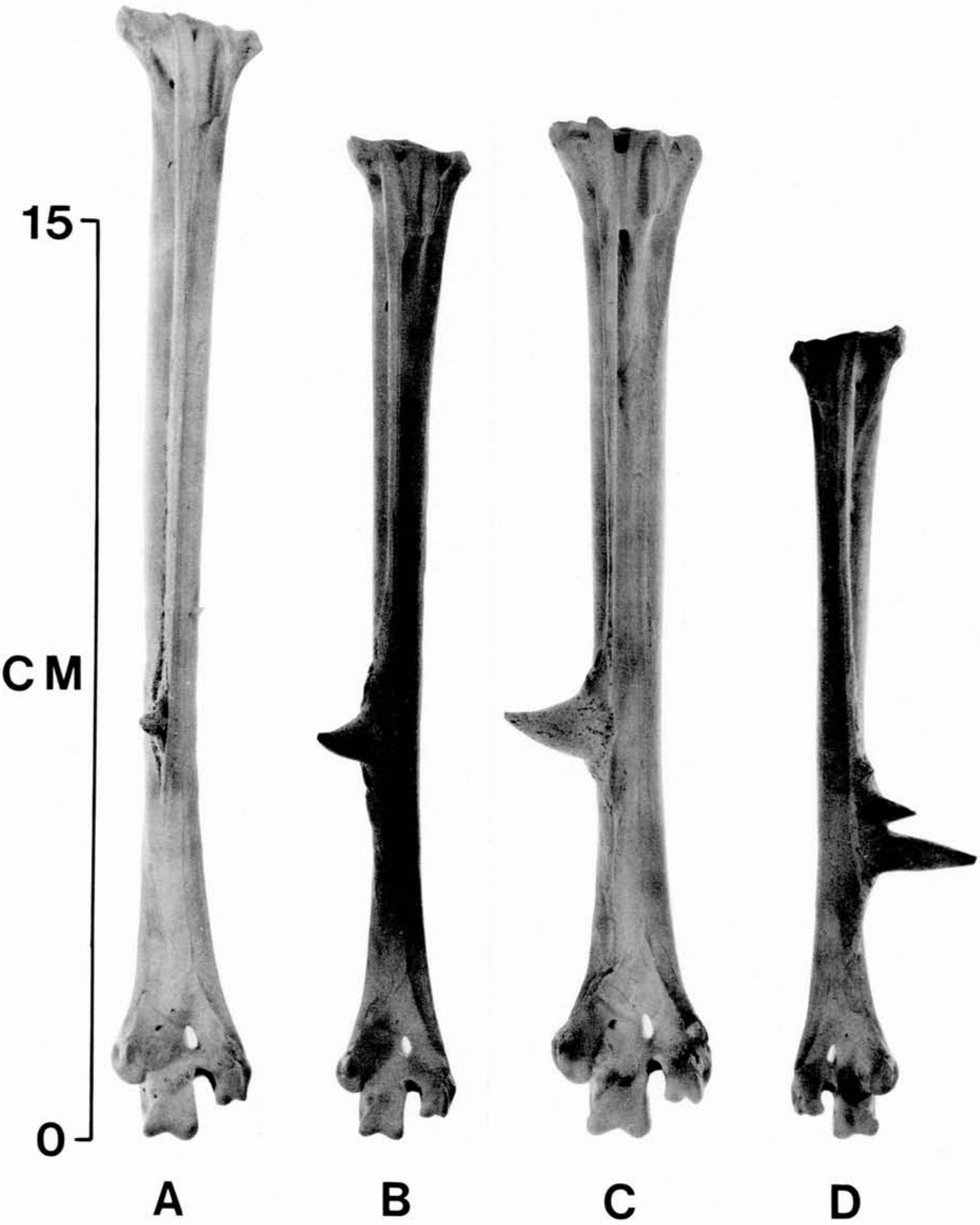


Figure 11. Posterior views of tarsometatarsi of males: A, B. *Meleagris gallopavo osceola* (PB 33819, PB 23117); C. *Meleagris gallopavo silvestris* (USNM 501686); D. *Meleagris ocellata* (PB 23542).

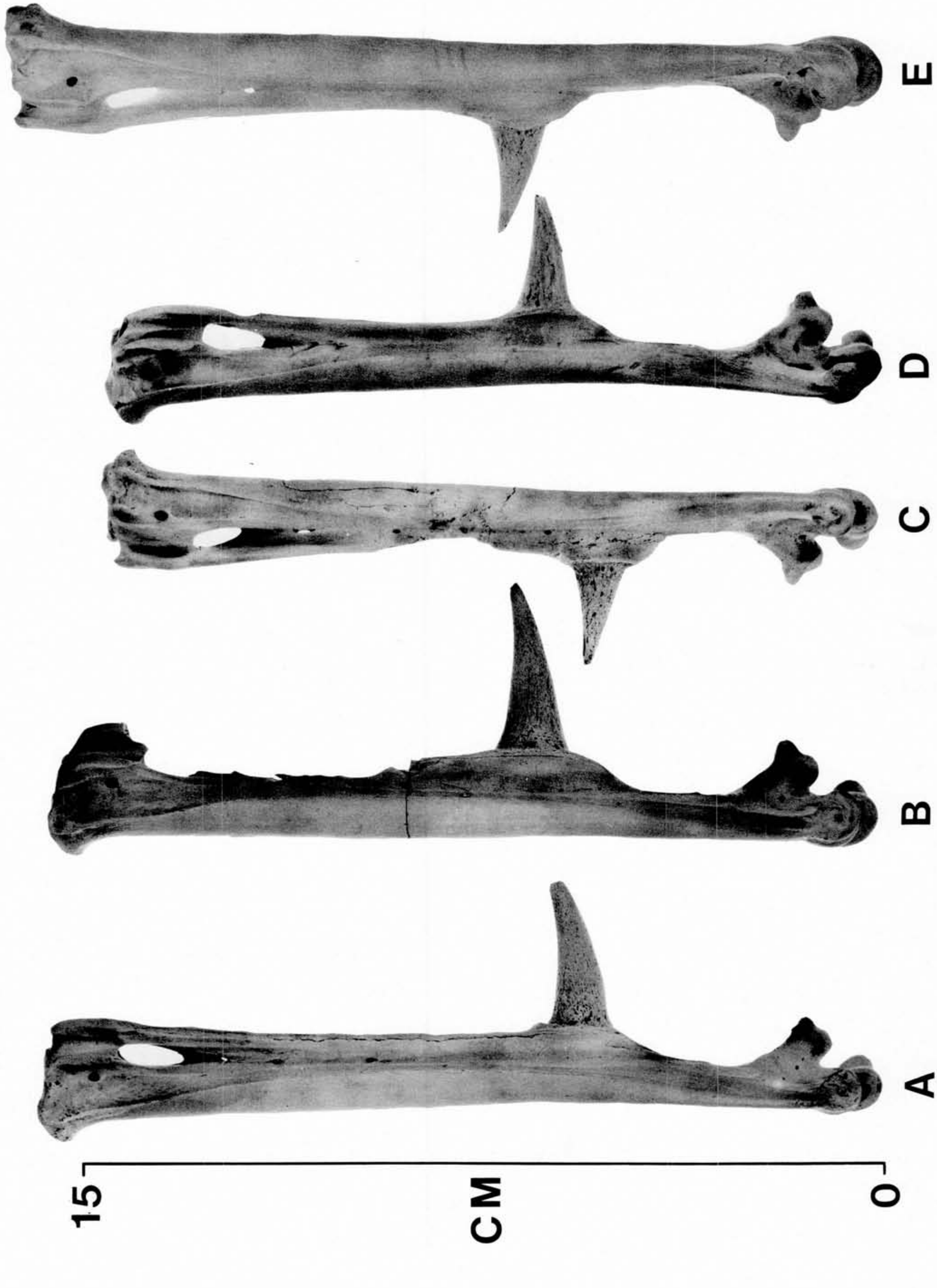


Figure 12. Lateral views of tarsometatarsi of males: A. *Meleagris* cf. *M. leopoldi* or *M. anza* (Inglis IA; UF 20713); B, C. *Meleagris* sp. (Coleman; UF 11601N, UF 11603C); D. *Meleagris californica* (Rancho La Brea; LACM E-5775); E. *Meleagris gallopavo silvestris* (USNM 501686).

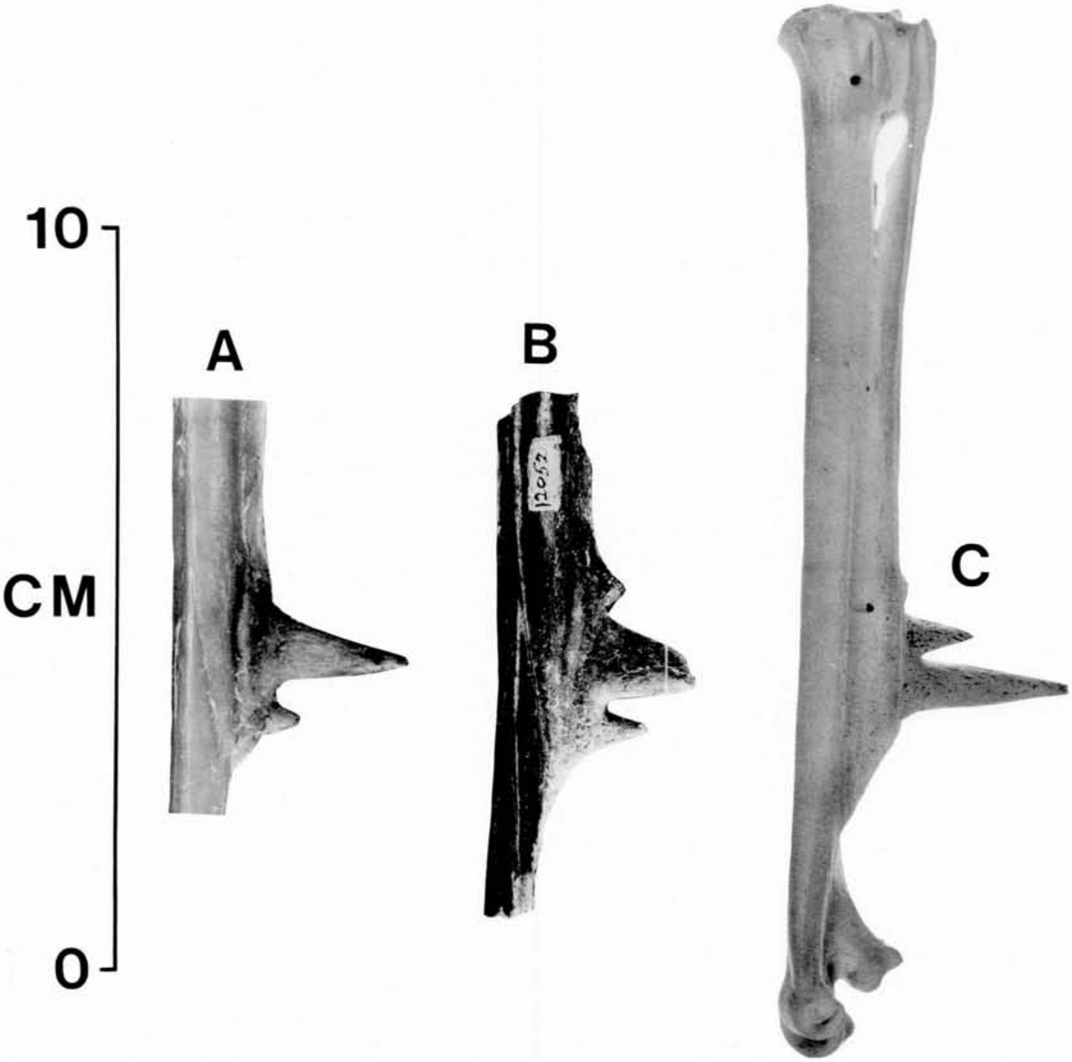


Figure 13. Medial views (A, B) and lateral view (C) tarsometatarsi of males: A. *Meleagris gallopavo osceola* (USNM 487663); B. *Meleagris gallopavo* (Seminole Field; USNM 12052—holotype of *Meleagris "tridens"*); C. *Meleagris ocellata* (PB 23542).

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Figure 14. Anterior views of tarsometatarsi of females: A, B, C. *Rhegminornis calobates* (Thomas Farm; PB 8448, PB 8447, MCZ 2331—not certainly females); D. *Proagriocharis kimballensis* (UNSM Coll. Loc. Ft-40; UNSM 20037); E. *Meleagris progenes* (Rexroad; UMMP 48189); F. *Meleagris crassipes* (San Josecito Cave; LACM UC-100022); G. *Meleagris* cf. *M. leopoldi* or *M. anza* (Inglis IA; UF 20789); H. *Meleagris* sp. (Coleman IIA; UF 11601Z); I. *Meleagris californica* (Rancho La Brea; LACM E-7122); J. *Meleagris gallopavo osceola* (PB 23114); K. *Meleagris ocellata* (PB 30884).

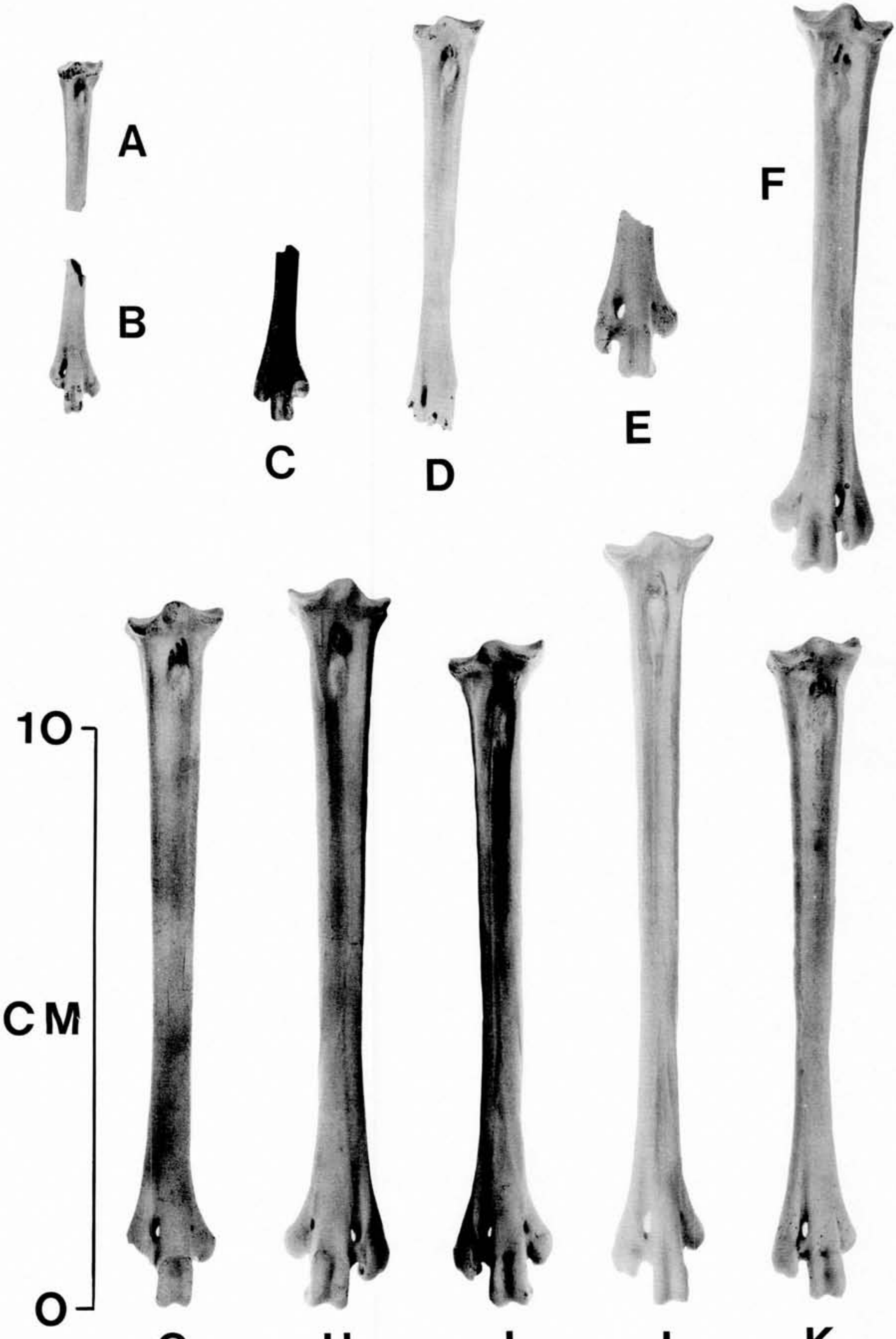
A
B
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Table 1. Fossil localities discussed in text. Numbered localities are shown in Fig. 1.

Fossil Locality	Age	Species of Turkey	References*
1. Thomas Farm, Florida	early Miocene (Hemingfordian)	*Rhegminornis calobates*	Olson and Farrand 1974; Patton 1969; Wetmore 1943.
2. Westmoreland State Park, Virginia	late Miocene (Clarendonian?)	Meleagridinae, cf. *Meleagris*	Lauck Ward pers. comm.; this paper.
3. UNSM Coll. Loc. Ft-40, Nebraska	late Miocene or early Pliocene (Hemphillian)	*Proagriocharis kimballensis*	Martin and Tate 1970.
4. Buckhorn, New Mexico	late Miocene or early Pliocene (Hemphillian)	Meleagridinae, cf. *Meleagris*	This paper.
5. Clifton Country Club, Arizona	late Miocene or early Pliocene (Hemphillian)	Meleagridinae, genus and species indeterminate	This paper.
6. Bone Valley (Palmetto Mine), Florida	late Miocene or early Pliocene (Hemphillian)	Meleagridinae, cf. *Meleagris*	This paper; G. Morgan pers. comm.
7. University Drive, California	Pliocene (Hemphillian or Blancan)	*Meleagris* sp.	This paper
8. Haile XVA, Florida	late Pliocene (Blancan)	*Meleagris* sp.	Campbell 1976; Robertson 1976; this paper.
9. Benson, Arizona	late Pliocene (Blancan)	*Meleagris* cf. *M. progenes*	Brodkorb 1964b; Lindsay et al. 1975; Wetmore 1924, 1944; this paper.
10. Cita Canyon, Texas	late Pliocene (Blancan)	*Meleagris leopoldi*	Brodkorb 1964b; Lindsay et al. 1975; A. Miller and Bowman 1956; this paper.
11. Rexroad, Kansas	late Pliocene (Blancan)	*Meleagris progenes*	Brodkorb 1964b; Lindsay et al. 1975; this paper.
12. Gilliland, Texas	early Pleistocene (early Irvingtonian)	Meleagridinae, genus and species indeterminate	Brodkorb 1964b; Hibbard and Dalquest 1973; this paper.
13. Inglis IA, Florida	early Pleistocene (early Irvingtonian)	*Meleagris* cf. *M. leopoldi* or *M. anza*	Klein 1971; Webb 1974; this paper.
14. Vallecito Creek, California	early Pleistocene (Irvingtonian)	*Meleagris anza*	Howard 1963; Opdyke et al. 1977; this paper.
15. Port Kennedy Cave, Pennsylvania	early Pleistocene (Irvingtonian; possibly Rancholabrean?)	Meleagridinae, cf. *Meleagris*	D. Gillette pers. comm.; Mercer 1899; this paper.
16. Haile XVIA, Florida	early Pleistocene (Irvingtonian)	*Meleagris* sp.	M. Frazier pers. comm.; this paper.
17. Williston, Florida	middle Pleistocene (late Irvingtonian)	*Meleagris* sp.	M. Frazier pers. comm.; this paper.
18. Coleman IIA, Florida	middle Pleistocene (late Irvingtonian)	*Meleagris* sp. (intermediate between *leopoldi-anza* and *gallopavo*)	Martin 1974; this paper.
19. Sante Fe River IIA, Florida	middle Pleistocene (late Irvingtonian)	*Meleagris* cf. *M. gallopavo*	Webb 1974; this paper.
20. American Falls Lake Beds, Idaho	late Pleistocene (Rancholabrean; Illinoian glacial?)	*Meleagris gallopavo*	Hopkins et al. 1969.
Papago Springs Cave, Arizona	late Pleistocene (Rancholabrean)	*Meleagris* sp.	Skinner 1942; Rea this volume; this paper.
Arizpe, Sonora, México	late Pleistocene (Rancholabrean)	*Meleagris* cf. *M. gallopavo*	Cracraft 1968; Rea this volume; this paper.
Burnet Cave, New Mexico	late Pleistocene (Rancholabrean)	*Meleagris* cf. *M. gallopavo*; also *M. crassipes*	Rea this volume; Schultz and Howard 1935; this paper.
Howell's Ridge Cave, New Mexico	late Pleistocene (Rancholabrean) and Holocene	*Meleagris* sp.; also *M. crassipes*	Rea this volume; Van Devender and Worthington 1977; this paper.
Ingleside, Texas	late Pleistocene (Rancholabrean)	*Meleagris gallopavo*	Feduccia 1973.
Sheffield Gravel Pits, Texas	late Pleistocene? (Rancholabrean?)	*Meleagris* sp	This paper.
Carlisle Cave, Pennsylvania	Pleistocene (probably Rancholabrean)	*Meleagris* cf. *M. gallopavo*	Leidy 1889; this paper.

Table 1. Continued.

Fossil Locality	Age	Species of Turkey	References*
Frankstown Cave, Pennsylvania	late Pleistocene (Rancholabrean)	*Meleagris* cf. *M. gallopavo*	Hibbard et al. 1965; Peterson 1926; this paper.
Manalapan, New Jersey	late Pleistocene? (Rancholabrean?)	*Meleagris gallopavo*	This paper.
Bradenton, Florida	late Pleistocene (early Rancholabrean)	*Meleagris* sp.	Webb 1974; this paper.
Rock Spring, Florida	late Pleistocene (early Rancholabrean)	*Meleagris* cf. *M. gallopavo*	Webb 1974; this paper.
Withlacoochee River, Florida	late Pleistocene (early Rancholabrean)	*Meleagris* sp.	Webb 1974; this paper.
Haile VIIA, Florida	late Pleistocene (early Rancholabrean)	*Meleagris* sp.	Webb 1974; this paper.
Reddick IB, Florida	late Pleistocene (early Rancholabrean)	*Meleagris* cf. *M. gallopavo*	Webb 1974; this paper.
Melbourne, Florida	late Pleistocene (middle Rancholabrean)	*Meleagris* cf. *M. gallopavo*	Webb 1974; this paper.
Arredondo, Florida	late Pleistocene (middle Rancholabrean)	*Meleagris* cf. *M. gallopavo*	Webb 1974; this paper.
Sabertooth Cave, Florida	late Pleistocene (late Rancholabrean)	*Meleagris* cf. *M. gallopavo*	Webb 1974; this paper.
Aucilla River, Florida	late Pleistocene (late Rancholabrean)	*Meleagris gallopavo*	Webb 1974; this paper.
Ichetucknee River, Florida	late Pleistocene (late Rancholabrean)	*Meleagris gallopavo*	Webb 1974; Wetmore 1931a.
Kendrick IA, Florida	late Pleistocene (late Rancholabrean)	*Meleagris* sp.	Webb 1974; this paper.
Vero, Florida	late Pleistocene (late Rancholabrean)	*Meleagris* cf. *M. gallopavo*	Webb 1974; this paper.
Seminole Field, Florida	late Pleistocene (late Rancholabrean)	*Meleagris gallopavo*	Webb 1974; Wetmore 1931a.
Bowman IA, Florida	late Pleistocene (Rancholabrean)	*Meleagris* cf. *M. gallopavo*	M. Frazier, S.D. Webb pers. comm.; this paper.
Davis Quarry, Florida	late Pleistocene (Rancholabrean)	*Meleagris gallopavo*	M. Frazier, S.D. Webb pers. comm.; this paper.
Econfina River, Florida	late Pleistocene (Rancholabrean)	*Meleagris* sp.	M. Frazier, S.D. Webb pers. comm.; this paper.
Florida Lime Company, Florida	late Pleistocene (Rancholabrean)	*Meleagris* sp.	M. Frazier, S.D. Webb pers. comm.; this paper.
Haile IIA, Florida	late Pleistocene (Rancholabrean)	*Meleagris* cf. *M. gallopavo*	M. Frazier, S.D. Webb pers. comm.; this paper.
Hog Creek, Florida	late Pleistocene (Rancholabrean)	*Meleagris* sp.	M. Frazier, S.D. Webb pers. comm.; this paper.
Mefford Cave I, Florida	late Pleistocene (Rancholabrean)	*Meleagris* cf. *M. gallopavo*	M. Frazier, S.D. Webb pers. comm.; this paper.
Oakhurst Quarry, Florida	late Pleistocene (Rancholabrean)	*Meleagris* sp.	M. Frazier, S.D. Webb pers. comm.; this paper.
St. Mark's River, Florida	late Pleistocene (Rancholabrean)	*Meleagris* sp.	M. Frazier, S.D. Webb pers. comm.; this paper.
Santa Fe River IA, Florida	late Pleistocene (Rancholabrean)	*Meleagris* cf. *M. gallopavo*	Webb 1974; this paper.
Santa Fe River IVA, Florida	late Pleistocene (Rancholabrean)	*Meleagris* sp.	M. Frazier, S.D. Webb pers. comm.; this paper.
Steinhatchie River, Florida	late Pleistocene (Rancholabrean)	*Meleagris* cf. *M. gallopavo*	M. Frazier, S.D. Webb pers. comm.; this paper.
Wekiva Run III, Florida	late Pleistocene (Rancholabrean)	*Meleagris* sp.	M. Frazier, S.D. Webb pers. comm.; this paper.
Wacissa River, Florida	Holocene	*Meleagris gallopavo*	This paper.

Continued

Table 1. Continued.

Fossil Locality	Age	Species of Turkey	References*
Nichol's Hammock, Florida	Holocene (pre-1900)	*Meleagris gallopavo*	Hirschfeld 1968.
Good's Shellpit, Florida	Holocene (approx. 3500–5000 BP)	*Meleagris gallopavo*	Neill et al. 1956.
Silver Glen Springs, Florida	Holocene (approx. 3500–5000 BP)	*Meleagris* sp.	Neill et al. 1956; this paper.
Buffalo Site, West Virginia	Holocene (approx. AD 1650)	*Meleagris gallopavo*	Kooliath 1975.
Hartman's Cave, Pennsylvania	Holocene (post-European contact)	*Meleagris gallopavo*	Leidy 1889; this paper.
21. Rancho La Brea, California	late Pleistocene (Rancholabrean)	*Meleagris californica*	Hibbard et al. 1965; this paper.
22. Imperial Highway, California	late Pleistocene (Rancholabrean)	*Meleagris* sp.	W. Miller 1971; this paper.
23. Carpinteria, California	late Pleistocene (Rancholabrean)	*Meleagris californica*	L. Miller 1927; Hibbard et al. 1965.
24. Workman and Alhambra Streets, California	late Pleistocene (Rancholabrean)	Meleagridinae cf. *Meleagris*	W. Miller 1971; this paper.
25. La Mirada, California	late Pleistocene (Rancholabrean)	*Meleagris* cf. *M. californica*	W. Miller 1971; this paper.
26. Potter Creek Cave, California	late Pleistocene (Rancholabrean)	*Meleagris* sp.	Hibbard et al. 1965; L. Miller 1911.
Dzibilchaltún, Yucatán, México	Holocene (approx. BC 1000-AD 900)	*Meleagris ocellata*	Wing and Steadman in press.
Mayapán, Yucatán, México	Holocene (approx. AD 1200–1500)	*Meleagris ocellata*	Pollock and Ray 1957.
Cancún Island, Quintana Roo, México	Holocene (approx. AD 300–900)	*Meleagris* cf. *M. ocellata*	This paper.
Tulúm, Quintana Roo, México	Holocene (approx. AD 1300–1500)	*Meleagris* cf. *M. ocellata*	This paper.
Barton Ramie site, Belize	Holocene (approx. AD 500–1000)	*Meleagris* cf. *M. ocellata*	Brodkorb 1964b; this paper.
Macanché, Petén, Guatemala	Holocene (approx. AD 300–900)	*Meleagris* cf. *M. ocellata*	This paper.
27. San Josecito Cave, Nuevo León, México	late Pleistocene (Rancholabrean)	*Meleagris crassipes*	Hibbard et al. 1965; L. Miller 1940.

* Includes only literature from which this table was compiled; see references cited in this table for additional literature on the fossil sites. Earlier published records of turkeys from these sites, if recorded under a different name, are mentioned in the site by site accounts.

Table 2. Analysis of similarity. For every character in the comparative osteology section, except those that are similar in all forms, each form was rated against the others as follows: 100 = complete agreement; 75 = much agreement; 50 = partial agreement; 25 = slight agreement; 0 = no agreement. The first value in each case is the mean of all such agreement values. The number in parentheses is the number of characters on which the mean agreement value is based.

	Rhegminornis calobates Thomas Farm, Florida	*Proagriocharis kimballensis* UNSM Coll. Loc. Ft-40, Nebraska	*Meleagris progenes* Rexroad, Kansas	*Meleagris leopoldi* Cita Canyon, Texas	*Meleagris anza,* Vallecito Creek, California	*Meleagris* cf *M. leopoldi* or *M. anza* Inglis IA Florida	*Meleagris* sp., Coleman IIA, Florida	*Meleagris gallopavo* Recent specimens	*Meleagris californica,* Rancho La Brea, California	*Meleagris ocellata* Recent specimens	*Meleagris crassipes* San Josecito Cave, Nuevo León, México
Proagriocharis kimballensis, UNSM Coll. Loc. Ft-40	75 (8)	—	—	—	—	—	—	—	—	—	—
Meleagris progenes Rexroad	59 (11)	50 (14)	—	—	—	—	—	—	—	—	—
Meleagris leopoldi Cita Canyon	71 (13)	84 (11)	92 (12)	—	—	—	—	—	—	—	—
Meleagris cf. *M. leopoldi* or *M. anza* Inglis IA	56 (13)	73 (21)	78 (30)	87 (17)	68 (7)	—	—	—	—	—	—
Meleagris sp. Coleman IIA	54 (13)	63 (21)	78 (26)	85 (17)	50 (7)	89 (64)	—	—	—	—	—
Meleagris gallopavo, Recent specimens	56 (13)	58 (21)	73 (30)	87 (17)	64 (7)	68 (73)	82 (65)	—	—	—	—
Meleagris californica, Rancho La Brea	54 (13)	54 (21)	75 (29)	82 (17)	57 (7)	78 (72)	82 (65)	80 (75)	—	—	—
Meleagris ocellata Recent specimens	48 (13)	58 (21)	72 (30)	78 (17)	57 (7)	68 (73)	72 (65)	62 (85)	72 (75)	—	—
Meleagris crassipes San Josecito Cave	52 (13)	46 (21)	73 (24)	69 (17)	57 (7)	74 (47)	72 (47)	73 (47)	79 (47)	62 (47)	—

Table 3. Analysis of similarity in the tarsometatarsus. See Table 2 for explanation of values.

	Rhegminornis calobates Thomas Farm, Florida	*Proagriocharis kimballensis* UNSM Coll. Loc. Ft-40, Nebraska	*Meleagris progenes* Rexroad, Kansas	*Meleagris leopoldi* Cita Canyon, Texas	*Meleagris* cf. *leopoldi* or *M. anza,* Inglis IA, Florida	*Meleagris* sp. Coleman IIA, Florida	*Meleagris gallopavo* Recent specimens	*Meleagris californica* Rancho La Brea, California	*Meleagris ocellata* Recent specimens	*Meleagris crassipes* San Josecito Cave, Nuevo León, México
Proagriocharis kimballensis UNSM Coll. Loc. Ft-40	75 (8)	—	—	—	—	—	—	—	—	—
Meleagris progenes Rexroad	59 (11)	83 (6)	—	—	—	—	—	—	—	—
Meleagris leopoldi Cita Canyon	71 (13)	84 (11)	92 (12)	—	—	—	—	—	—	—
Meleagris cf. *M. leopoldi* or *M. anza* Inglis IA	56 (13)	77 (12)	96 (12)	87 (17)	—	—	—	—	—	—
Meleagris sp. Coleman IIA	54 (13)	73 (12)	94 (12)	85 (17)	96 (18)	—	—	—	—	—
Meleagris gallopavo Recent specimens	56 (13)	71 (12)	98 (12)	87 (17)	89 (18)	93 (18)	—	—	—	—
Meleagris californica Rancho La Brea	54 (13)	67 (12)	94 (12)	82 (17)	83 (18)	88 (18)	92 (18)	—	—	—
Meleagris ocellata Recent specimens	48 (13)	79 (12)	83 (12)	78 (17)	79 (18)	78 (18)	76 (18)	72 (18)	—	—
Meleagris crassipes San Josecito Cave	52 (13)	56 (12)	83 (12)	69 (17)	72 (18)	74 (18)	78 (18)	85 (18)	58 (18)	—

Table 4. Measurements (in mm) of coracoids of male turkeys, with mean, standard deviation, observed range, and sample size. See Fig. 2 for explanation of measurements.

	Head to External End of Sternal Facet	Head to Internal Distal Angle	Head to Pneumatic Foramen	Head through Scapular Facet	Depth of Head	Least Width of Shaft
Proagriocharis kimballensis UNSM Coll. Loc. Ft-40	71.7* 1	67.2* 1	57.9* 1	23.1* 1	9.1 1	6.4 1
Meleagridinae, genus and species indet. Clifton Country Club[a]	—	—	—	24.5 1	9.8 1	~8.2 1
Meleagris progenes Rexroad	79.8* 1	—	65.0[b] 1	31.0[b] 1	10.8[b] 1	10.1[b] 1
Meleagris cf. *M. leopoldi* or *M. anza* Inglis IA	101.93 94.2–110.7 6	94.26* ± 2.52 80.4–97.4* 10	76.21 ± 2.54 72.6–80.2 8	35.95 ± 1.27 33.9–37.8 13	13.62 ± 0.86 11.8–15.0 20	10.44 ± 0.45 9.6–11.2 27
Meleagris sp. Coleman IIA	103.72* 101.2–105.4* 5	97.30 95.3–99.0 4	79.35 76.0–80.8 4	37.80 37.0–38.7 7	14.84 ± 0.49 14.2–15.8 8	11.12 ± 0.84 10.0–11.9 8
M. gallopavo Ingleside	115.2* 1	—	—	40.8 1	15.5 1	10.8 1
M. gallopavo Manalapan	118.5 115[c]–122[d] 2	—	90.0 1	43.2 1	16.2 1	12.6 1
M. gallopavo Ichetucknee River	117.05* 113.9*–120.2 2	110.10 108.3–111.9 2	89.40 87.1–91.7 2	41.18 39.1–42.7 5	15.55 14.1–17.0 6	11.83 11.4–12.3 3
M. gallopavo Seminole Field	—	—	—	38.1 1	14.6 1	—
M. gallopavo Davis Quarry	104.30* 101.0*–107.6* 2	97.25* 94.8*–99.7* 2	77.10* 75.5–78.7* 2	37.95* 36.3–39.6* 2	14.55 13.5–15.6 2	11.30 11.0–11.6 2
Meleagris cf. *M. gallopavo* Mefford Cave I	—	—	—	41.7* 1	16.6 1	—
M. gallopavo Nichol's Hammock	—	—	—	39.1* 1	14.2 1	—
M. gallopavo Good's Shellpit	106.5 1	98.6 1	82.0 1	37.7 1	14.3 1	9.7 1
M. gallopavo Garfield Site	112.7* 1	102.8* 1	85.8* 1	40.0* 1	14.6 1	10.9 1
M. gallopavo Buffalo Site	115.19 ± 2.97 110.0–118.5 12	108.12 ± 1.98 103.7–111.0 9	88.94 ± 3.67 83.2–97.5 16	41.68 ± 1.00 39.9–43.3 27	16.15 ± 0.85 14.1–17.7 27	11.71 ± 0.46 10.5–13.3 81
M. gallopavo Hartman's Cave	112.3 1	106.8* 1	91.0 1	40.8 1	16.0 1	10.4 1
M. gallopavo silvestris New York, Pennsylvania, Virginia	112.37 ± 4.14 104.2–120.8 26	104.79 ± 3.89 97.2–111.5 27	85.12 ± 3.39 77.8–90.4 27	40.71 ± 1.33 38.4–43.1 27	15.94 ± 0.64 14.6–17.2 28	11.29 ± 0.54 10.2–12.5 28
M. gallopavo osceola Florida	109.19 ± 4.29 104.9–117.0 9	101.19 ± 3.90 97.1–107.3 9	83.01 ± 2.94 80.0–89.5 9	37.94 ± 1.33 35.2–39.9 9	14.50 ± 0.77 13.3–15.9 9	10.68 ± 0.45 10.0–11.2 9
M. gallopavo intermedia Texas	114.7 1	—	87.3 1	38.6 1	15.1 1	10.9 1
M. gallopavo mexicana Chihuahua, México	113.65 111.8–115.5 2	104.70 103.0–106.4 2	83.15 81.5–84.8 2	40.40 39.8–41.0 2	16.00 15.6–16.4 2	11.35 10.8–11.9 2
M. gallopavo Total skeletal specimens	111.74 ± 4.25 104.2–120.8 38	103.93 ± 4.06 97.1–111.5 38	84.59 ± 3.31 77.8–90.4 39	40.00 ± 1.74 35.2–43.1 39	15.60 ± 0.89 13.3–17.2 40	11.15 ± 0.57 10.0–12.5 40

Continued

Table 4. Continued

	Head to External End of Sternal Facet	Head to Internal Distal Angle	Head to Pneumatic Foramen	Head through Scapular Facet	Depth of Head	Least Width of Shaft
M. californica Rancho La Brea	101.01 ± 3.97 92.0–106.1 15	94.26* ± 3.06 85.8*–98.8 29	76.54 ± 3.44 68.2–82.4 27	35.94 ± 1.19 32.3–38.2 29	13.21 ± 0.85 11.7–14.6 24	10.08 ± 0.46 9.1–11.0 29
M. californica Carpinteria	99.17 96.7–101.4 7	92.42* ± 2.11 89.4–94.9 8	74.34 72.7–76.4 7	35.16 ± 1.09 33.5–37.3 8	13.61 ± 0.72 12.4–14.8 8	10.02 ± 0.48 9.2–10.6 8
M. californica Total specimens	100.42 ± 3.48 92.0–106.1 22	93.86* ± 2.96 85.8*–98.8 37	76.08 ± 3.24 68.2–82.4 34	35.78 ± 1.20 32.3–38.2 37	13.31 ± 0.82 11.7–14.8 32	10.07 ± 0.46 9.1–11.0 37
M. ocellata Dzibilchaltún	93.4* 1	87.7 1	70.9 1	34.0 1	12.55 12.4–12.7 2	9.1 1
M. ocellata Mayapán	95.0 1	88.45 87.3–89.6 2	70.09 ± 2.23 67.2–73 2 10	32.74 ± 1.28 30.0–34.9 21	12.26 ± 0.68 10.9–13.3 21	9.14 ± 0.56 8.2–10.2 13
M. ocellata Yucatán, México and Petén, Guatemala	89.25 ± 3.90 81.3–93.7 10	84.08 ± 3.21 78.9–87.7 10	68.43 ± 3.17 62.0–72 2 10	31.99 ± 1.31 30.0–34.1 8	12.03 ± 0.74 10.6–12.9 10	8.81 ± 0.61 7.9–9.8 10
M. crassipes San Josecito Cave	79.6* 1	76.0* 1	—	29.1 1	9.8 1	8.3 1

[a] May possibly represent a female; [b] from Brodkorb 1964b; [c] from Cope 1871; [d] from Marsh 1872. Probably the same bone measured by Shufeldt (1915).

* Slightly damaged specimens.

Table 5. Measurements (in mm) of the coracoid of female turkeys, with mean, standard deviation, observed range, and sample size. See Fig. 2 for explanation of measurements.

	Head to External End of Sternal Facet	Head to Internal Distal Angle	Head to Pneumatic Foramen	Head through Scapular Facet	Depth of Head	Least Width of Shaft
Meleagridinae, genus and species indet. Gilliland	72.0** 1	70.4** 1	—	—	—	7.9 1
Meleagris cf. *M. leopoldi* or *M. anza* Inglis IA	77.90* 76.9*–78.9* 2	75.20* 74.7*–75.7* 2	60.73* 60.2*–61.1* 3	—	10.30 10.0–10.6 2	8.40 8.3–8.6 5
Meleagris sp. Coleman IIA	86.25 83.7–88.8 2	80.50 78.2–82.8 2	66.95 64.2–69.7 2	31.40 31.0–31.8 2	11.85 11.8–11.9 2	8.95 8.7–9.2 2
Meleagris cf. *M. gallopavo* Rock Spring	—	—	—	31.20 30.8–31.6 2	11.55 11.5–11.6 2	—
Meleagris cf. *M. gallopavo* Reddick IB	—	—	—	31.0 1	12.1 1	—
M. gallopavo Ichetucknee River	86.45* 83.1–89.8* 2	81.95* 79.9–84.0* 2	65.35 65.3–65.4 2	31.30 30.4–32.1 3	11.70 11.2–12.2 4	9.20 8.9–9.7 4
M. gallopavo Seminole Field	—	—	64.8 1	31.05 30.0–32.1 2	10.2 1	8.35 8.1–8.6 2

Table 5. Continued.

	Head to External End of Sternal Facet	Head to Internal Distal Angle	Head to Pneumatic Foramen	Head through Scapular Facet	Depth of Head	Least Width of Shaft
Meleagris sp. Florida Lime Company	—	77.5* 1	63.5* 1	30.1* 1	11.1* 1	8.2 1
M. gallopavo Nichol's Hammock	81.25 81.2–81.3 2	76.00* 75.8*–76.2 2	62.57* 59.6*–64.1 3	28.33* 28.0*–28.6 3	10.57 9.8–11.0 3	8.08 8.0–8.2 4
M. gallopavo Good's Shellpit	83.9 1	77.6 1	62.3 1	29.2 1	10.8 1	8.0 1
M. gallopavo Buffalo Site	92.11 ± 2.29 86.1–96.1 15	86.22 ± 2.37 80.7–91.5 16	70.11 ± 2.27 65.4–74.0 15	32.74 ± 1.09 30.2–35.3 32	12.44 ± 0.64 10.8–13.7 31	9.25 ± 0.45 7.9–10.5 56
M. gallopavo silvestris New York, Pennsylvania, Virginia	87.68 ± 1.71 85.8–90.2 13	81.57 ± 1.71 80.0–84.7 12	66.51 ± 1.88 64.2–71.0 13	32.18 ± 0.33 31.6–32.7 13	12.08 ± 0.46 11.3–13.0 13	8.78 ± 0.48 8.1–9.6 13
M. gallopavo osceola Florida	83.40 ± 2.24 80.6–88.0 10	77.92 ± 2.18 74.7–82.7 10	63.73 ± 2.23 60.7–67.6 11	29.73 ± 1.10 28.0–31.6 11	10.94 ± 0.76 10.0–12.4 11	8.37 ± 0.49 7.8–9.3 11
M. gallopavo intermedia Texas	85.8* 1	80.5* 1	65.9* 1	31.1* 1	12.0 1	8.2 1
M. gallopavo mexicana Chihuahua, Coahuila, México	87.80 85.2–92.5 3	81.77 79.3–86.3 3	65.37 63.3–68.4 3	31.83 30.0–34.2 3	12.57 11.6–13.8 3	8.70 8.2–9.0 3
M. gallopavo merriami Arizona	88.67 85.2–90.6 3	83.00 79.6–85.0 3	66.70 63.3–70.2 3	31.53 31.0–31.8 3	11.50 11.1–11.9 3	8.50 8.2–8.7 3
M. gallopavo Total skeletal specimens[a]	86.10 ± 3.24 79.8–92.5 31	80.21 ± 3.11 73.7–86.3 30	65.16 ± 2.79 58.1–71.0 32	31.08 ± 1.52 28.0–34.2 32	11.64 ± 0.84 10.0–13.8 32	8.56 ± 0.48 7.8–9.6 32
M. californica Rancho La Brea	81.64 ± 3.42 73.1–84.8 11	76.16 ± 2.50 68.9–79.2 27	61.84 ± 2.24 56.7–66.1 25	28.85 ± 1.06 25.4–30.2 24	10.86 ± 0.60 9.5–11.8 27	8.08 ± 0.47 6.8–8.8 27
M. californica Carpinteria	—	—	—	29.46 28.3–30.0 7	11.13 10.6–11.7 7	8.25 8.0–8.5 4
M. californica Total specimens	81.64 ± 3.42 73.1–89.1 11	76.16 ± 2.50 68.9–79.2 27	61.84 ± 2.24 56.7–66.1 25	28.99 ± 1.00 25.4–30.2 31	10.92 ± 0.57 9.5–11.8 34	8.10 ± 0.44 6.8–8.8 31
Meleagris sp. Potter Creek Cave	—	73.9* 1	59.8* 1	29.4* 1	10.2 1	7.8 1
M. ocellata Dzibilchaltún	—	—	—	—	—	7.5 1
M. ocellata Mayapán	80.9 1	73.60 71.7–75.7 4	59.38 56.9–61.2 5	26.86 ± 2.40 22.2–29.1 11	10.14 ± 0.72 9.0–11.1 11	7.61 ± 0.74 6.2–8.7 11
M. ocellata Yucatán, México and Petén, Guatemala	77.76 ± 1.94 74.8–80.8 10	72.93 ± 1.73 70.6–75.9 11	59.04 ± 1.97 55.5–61.6 11	26.74 ± 0.71 25.9–28.0 9	10.05 ± 0.46 9.1–11.0 11	7.39 ± 0.32 7.0–7.9 11
M. crassipes San Josecito Cave	—	67.30* 65.1*–68.7* 3	57.10* 55.4*–58.8 2	25.60 25.1–25.9 3	8.83 8.5–9.1 3	6.90 6.2–7.7 3

[a] Includes one specimen from northern Florida not identified to subspecies.

* Slightly damaged specimen.

** Moderately damaged specimen.

Table 6. Measurements (in mm) of the scapula of male turkeys, with mean, standard deviation, observed range, and sample size. See Fig. 2 for explanation of measurements.

	Proximal Width	Tip of Acromion to External Tip of Glenoid Facet	Depth of Glenoid Facet	Least Width of Neck
Meleagris cf. *M. leopoldi* or *M. anza* Inglis IA	22.94 ± 0.54 22.1–24.2 11	26.26 ± 0.74 25.6–27.9 8	10.33 ± 0.51 9.6–11.2 15	11.36 ± 0.54 10.5–12.3 17
Meleagris sp. Coleman IIA	25.57 24.1–26.6 3	28.83 27.4–29.6 3	11.20 10.8–11.8 3	12.50 12.2–12.8 4
M. gallopavo Manalapan	28.5 1	31.8 1	12.1* 1	14.0 1
Meleagris cf. *M. gallopavo* Melbourne	26.50* 25.6*–27.4 2	28.95* 28.1*–29.8 2	11.00 10.9–11.1 2	13.5 1
M. gallopavo Ichetucknee River	—	—	10.7 1	12.0 1
Meleagris cf. *M. gallopavo* Mefford Cave	28.6 1	31.2 1	11.9 1	14.7 1
M. gallopavo Buffalo Site	28.34 26.9–29.2 5	31.58 30.2–32.4 6	12.26 ± 0.64 11.2–13.2 13	14.50 ± 0.48 13.7–15.4 12
M. gallopavo silvestris, New York Pennsylvania, Virginia	27.56 ± 0.93 25.4–29.3 29	31.00 ± 1.09 29.0–33.0 27	12.38 ± 0.76 10.9–13.4 16	13.81 ± 0.90 12.1–16.0 29
M. gallopavo osceola Florida	25.61 ± 0.80 24.0–26.5 8	28.82 ± 1.06 27.1–30.1 8	11.51 ± 0.55 10.9–12.2 8	12.66 ± 0.76 11.2–13.5 8
M. gallopavo intermedia, Texas	—	29.3 1	—	13.0 1
M. gallopavo mexicana Chihuahua, México	27.7 1	30.1 1	12.5 1	14.6 1
M. gallopavo merriami, Arizona	27.0 1	29.6 1	11.1 1	13.2 1
M. gallopavo Total skeletal specimens	27.15 ± 1.18 24.0–29.3 39	30.44 ± 1.38 27.1–33.0 38	12.06 ± 0.78 10.9–13.4 26	13.56 ± 0.96 11.2–16.0 40
M. californica Rancho La Brea	23.66 ± 0.72 22.4–25.2 16	26.17 ± 0.78 24.8–27.9 16	10.56 ± 0.50 9.6–11.3 23	12.04 ± 0.87 10.8–13.8 14
M. californica Carpinteria	23.80 23.5–24.4 5	26.75 26.5–26.9 4	10.78 9.6–12.0 6	11.85 11.7–12.0 2
M. californica Total specimens	23.69 ± 0.66 22.4–25.2 21	26.28 ± 0.74 24.8–27.9 20	10.60 ± 0.58 9.6–12.0 29	12.01 ± 0.82 10.8–13.8 16
M. ocellata Mayapán	21.75 ± 0.68 20.7–22.8 12	24.80 ± 0.73 23.8–26.0 14	9.92 ± 0.34 9.3–10.7 28	11.14 ± 0.56 10.1–12.2 18
M. ocellata Yucatán, México and Petén, Guatemala	20.14 ± 1.29 18.7–22.5 10	22.96 ± 1.28 21.1–25.1 10	9.38 8.9–10.2 7	10.23 ± 0.83 9.4–11.9 10

* Slightly damaged specimen.

Table 7. Measurements (in mm) of the scapula of female turkeys, with mean, standard deviation, observed range, and sample size. See Fig. 2 for explanation of measurements.

	Proximal Width	Tip of Acromion to External Tip of Glenoid Facet	Depth of Glenoid Facet	Least Width of Neck
Meleagris progenes Rexroad	15.9 1	17.9* 1	7.9 1	—
Meleagris cf. *M. leopoldi* or *M. anza* Inglis IA	17.1 1	23.8 1	8.1 1	9.2 1
Meleagris sp. Haile XVIA	21.15* 20.1*–22.2 2	23.40* 22.3*–24.5 2	9.45 8.7–10.2 2	10.30 9.5–11.1 2
Meleagris sp. Coleman IIA	22.2 1	24.6 1	9.4 1	—
Meleagris cf. *M. gallopavo* Reddick IB	—	—	9.1 1	—
M. gallopavo Seminole Field	20.0 1	22.0 1	8.1 1	—
M. gallopavo Nichol's Hammock	19.87 18.9–20.5 3	22.20 21.2–23.0 3	8.33 7.9–9.1 3	9.7 9.7–9.9 3
Meleagris sp. Howell's Ridge Cave	22.0* 1	—	9.6 1	~12.0 1
M. gallopavo Buffalo Site	22.43 22.1–23.0 3	25.23 24.4–26.4 3	9.70 9.1–10.2 7	11.08 10.8–11.3 5
M. gallopavo silvestris, New York, Pennsylvania, Virginia	21.87 ± 0.36 21.0–22.3 12	24.30 ± 0.49 23.2–25.0 12	9.63 9.0–10.3 6	10.32 ± 0.54 9.4–11.1 12
M. gallopavo osceola Florida	20.18 ± 0.64 18.9–21.1 11	22.77 ± 0.54 22.0–23.8 11	8.75 ± 0.32 7.9–9.1 11	9.97 ± 0.59 9.0–11.0 11
M. gallopavo mexicana Chihuahua, Coahuila, México	21.30 20.0–22.6 3	23.60 22.2–24.9 3	9.40 9.0–10.0 3	10.23 9.9–10.6 3
M. gallopavo merriami Arizona	21.23 20.5–21.8 3	23.33 22.3–24.1 3	9.53 9.2–9.9 3	10.30 10.0–10.7 3
M. gallopavo Total skeletal specimens[a]	21.03 ± 1.03 18.9–22.6 30	23.46 ± 1.05 20.8–25.0 30	9.13 ± 0.60 7.9–10.3 24	10.15 ± 0.55 9.0–11.1 30
M. californica Rancho La Brea	19.25 ± 0.78 17.9–21.2 19	21.82 ± 0.94 20.7–24.6 18	8.70 ± 0.50 7.8–10.0 21	9.40 ± 0.48 8.7–10.8 22
M. californica Carpinteria	19.53 19.0–19.8 3	22.10 22.0–22.2 4	8.98 8.5–9.4 4	9.50 8.9–9.9 3
M. californica Total specimens	19.29 ± 0.74 17.9–21.2 22	21.87 ± 0.85 20.7–24.6 22	8.74 ± 0.49 7.8–10.0 25	9.41 ± 0.48 8.7–10.8 25
M. ocellata Mayapán	17.78 16.7–19.0 7	20.42 19.3–21.7 6	8.18 ± 0.42 7.6–8.8 10	8.72 ± 0.44 8.1–9.2 10
M. ocellata Yucatán, México and Petén, Guatemala	17.34 ± 0.40 16.8–18.9 11	19.51 ± 0.54 19.0–20.5 11	8.16 ± 0.27 7.6–8.5 9	8.86 ± 0.64 7.9–9.8 11

[a] Includes one specimen from northern Florida not identified to subspecies.

* Slightly damaged specimen.

Table 8. Measurements (in mm) of the humerus of male turkeys, with mean, standard deviation, observed range, and sample size. See Fig. 3 for explanation of measurements.

	Total Length	Proximal Width	Width of Midshaft	Depth of Midshaft	Distal Width
Meleagris cf. *M.* *leopoldi* or *M. anza* Inglis IA	136.69 ± 1.97 132.0–141.0 18	36.42 ± 0.89 34.9–38.6 22	15.00 ± 0.55 14.2–16.1 30	11.58 ± 0.42 10.9–12.3 29	30.05 ± 0.91 28.0–32.0 23
Meleagris sp. Haile XVIA	—	—	—	—	28.1 1
Meleagris sp. Coleman IIA	141.72 136.9–146.8 6	36.83 33.6–37.8 7	15.21 14.0–15.9 7	12.04 11.2–12.4 7	31.30 ± 0.52 30.0–31.9 14
Meleagris cf. *M.* *gallopavo*, Arizpe	—	38.9 1	—	—	—
Meleagris cf. *M.* *gallopavo* Burnet Cave	—	—	16.1 1	12.3 1	—
Meleagris sp. (juv.) North Liberty	131 1	—	—	—	—
M. gallopavo Carlisle Cave	—	42.3 1	—	—	—
Meleagris cf. *M.* *gallopavo* Frankstown Cave	—	—	—	—	31.4 1
M. gallopavo Manalapan	153.25 147.0[a]–159.5[b] 2	42[b] 1	—	—	33[b] 1
Meleagris cf. *M.* *gallopavo* Reddick IB	—	39.2 1	16.6 1	13.1 1	—
Meleagris cf. *M.* *gallopavo* Melbourne	—	—	—	—	30.1 1
Meleagris cf. *M.* *gallopavo* Arredondo	149.0 1	—	15.9 1	12.9 1	32.7 1
M. gallopavo Aucilla River	144.5 1	39.6 1	15.9 1	12.0 1	32.1 1
M. gallopavo Ichetucknee River	—	39.30 38.0–40.6 2	—	—	33.10 32.1–34.6 3
M. gallopavo Seminole Field	—	—	—	—	32.5 1
M. gallopavo Good's Shellpit	—	36.9 1	15.95 15.7–16.2 2	11.65 11.6–11.7 2	—
M. gallopavo Buffalo Site	157.1 ± 5.3 147–166 11	42.11 ± 0.99 39.4–44.0 28	16.63 ± 0.79 14.8–18.3 107	12.59 ± 0.59 11.1–14.1 108	33.59 ± 1.01 32.0–35.5 31
M. gallopavo Hartman's Cave	157.0 1	—	17.0 1	13.7 1	—
M. gallopavo silvestris, New York, Pennsylvania, Virginia	150.67 ± 3.38 144.0–159.0 28	40.75 ± 1.14 39.0–43.2 28	16.17 ± 0.84 14.2–17.4 29	12.56 ± 0.66 11.2–13.8 29	32.69 ± 0.84 31.3–34.3 27
M. gallopavo osceola Florida	148.31 ± 6.63 138.0–159.5 8	38.42 ± 1.54 36.0–40.8 8	15.65 ± 0.71 14.9–16.4 8	12.31 ± 0.54 11.5–13.1 8	31.18 ± 1.10 29.1–33.0 8
M. gallopavo intermedia Texas	156.0 1	39.2 1	16.2 1	12.6 1	31.8 1
M. gallopavo mexicana Chihuahua, México	152.5 1	40.5 1	17.3 1	13.3 1	34.1 1
M. gallopavo merriami, Arizona	149.5 1	39.3 1	15.7 1	12.1 1	31.4 1
M. gallopavo Total skeletal specimens	150.33 ± 4.26 138.0–159.5 39	40.19 ± 1.52 36.0–43.2 39	16.08 ± 0.83 14.2–17.4 40	12.52 ± 0.63 11.2–13.8 40	32.35 ± 1.11 29.1–34.3 38

Table 8. Continued.

	Total Length	Proximal Width	Width of Midshaft	Depth of Midshaft	Distal Width
M. californica Rancho La Brea	135.99 ± 4.24 128.0–142.5 34	35.35 ± 1.21 33.3–38.5 34	14.79 ± 0.65 13.3–15.9 34	11.70 ± 0.56 10.8–12.8 34	29.32 ± 0.96 26.7–30.8 34
M. californica Carpinteria	137.00 134.1–138.5 5	36.32 ± 0.60 35.5–37.0 8	14.98 14.7–15.6 5	12.02 11.4–12.7 5	29.75 ± 0.26 29.2–30.0 8
M. californica Total specimens	136.12 ± 4.00 128.0–142.5 39	35.54 ± 1.18 33.3–38.5 42	14.82 ± 0.62 13.3–15.9 39	11.74 ± 0.55 10.8–12.8 39	29.40 ± 0.88 26.7–30.8 42
M. ocellata Dzibilchaltún	130.0 1	32.65 31.7–33.6 2	13.7 1	10.9 1	27.8 1
M. ocellata Mayapán	127.38 ± 2.17 123.0–129.5 8	33.63 ± 0.60 32.6–34.6 11	13.24 12.3–14.0 5	10.10 9.4–10.9 5	27.53 26.7–28.2 6
M. ocellata Yucatán, México and Petén, Guatemala	123.77 ± 3.98 118.0–130.5 9	32.51 ± 1.34 30.5–34.9 9	12.68 ± 0.73 11.1–13.5 9	10.09 ± 0.86 8.7–11.7 9	26.60 ± 1.58 24.2–28.9 9
M. crassipes San Josecito Cave	119.07 117.1–120.2 3	30.93 30.6–31.2 3	12.10 11.3–12.7 3	9.70 9.2–10.5 3	25.40 25.2–25.6 2

[a] From Shufeldt 1915; [b] from Marsh 1872.

Table 9. Measurements (in mm) of the humerus of female turkeys, with mean, standard deviation, observed range, and sample size. See Fig. 3 for explanation of measurements.

	Total Length	Proximal Width	Width of Midshaft	Depth of Midshaft	Distal Width
Meleagris cf. *M. leopoldi* or *M. anza* Inglis IA	112.0 1	29.18 26.9–30.3 5	12.42 11.8–13.2 4	9.38 9.0–9.7 4	24.38 24.2–24.7 4
Meleagris anza Vallecito Creek[a]	112.4 1	~30.3 1	14.3 1	8.5 1	~24.0 1
Meleagris sp. Coleman IIA	119.8* 1	31.33* 30.1*–32.0 3	13.4 1	10.8 1	25.70 24.8–26.2 3
Meleagris sp. Papago Springs Cave[b]	122.0 1	31.4 1	13.9 1	10.5 1	26.30 26.2–26.4 2
Meleagris cf. *M. gallopavo* Carlisle Cave	125.50 124.0–127.0 2	32.45 32.2–32.7 2	13.70 13.3–14.1 2	10.65 10.3–11.0 2	26.40 26.2–26.6 2
Meleagris cf. *M. gallopavo* Rock Spring	—	—	—	—	24.9 1
M. gallopavo Ichetucknee River	121.25* 118.7*–123.8 2	31.35 30.9–31.8 2	12.68 11.9–14.0 4	9.87 9.2–10.6 3	26.35 25.2–27.0* 4
M. gallopavo Seminole Field	—	—	—	—	25.75 25.0–26.5 2

Continued

Table 9. Continued.

	Total Length	Proximal Width	Width of Midshaft	Depth of Midshaft	Distal Width
M. gallopavo Good's Shellpit	120.4 1	29.4 1	12.95 12.9–13.0 2	9.95 9.8–10.1 2	24.85 24.5–25.2 2
M. gallopavo Buffalo Site	127.7 ± 3.4 123–133 12	32.67 ± 0.86 30.9–33.9 21	13.26 ± 0.55 11.3–14.2 115	10.05 ± 0.48 8.0–11.1 115	26.86 ± 0.59 25.9–28.2 29
M. gallopavo Hartman's Cave	131.0 1	34.1 1	14.05 13.5–14.6 2	10.80 10.7–10.9 2	27.9 1
M. gallopavo silvestris, New York, Pennsylvania, Virginia	121.84 ± 2.29 117.0–125.0 13	32.15 ± 0.42 31.7–33.3 13	12.51 ± 0.56 11.7–13.2 13	9.53 ± 0.51 8.9–10.3 13	26.08 ± 0.38 25.3–26.8 13
M. gallopavo osceola, Florida	116.14 ± 2.77 111.2–120.2 11	29.79 ± 0.81 28.2–31.2 11	12.27 ± 0.45 11.5–12.9 11	9.42 ± 0.28 8.9–9.8 11	24.53 ± 0.79 22.9–25.8 11
M. gallopavo intermedia, Texas	120.8 1	32.0 1	12.4 1	9.9 1	26.1 1
M. gallopavo mexicana, Chihuahua, Coahuila, México	124.50 121.0–129.8 3	32.47 31.0–34.1 3	13.27 12.9–13.8 3	9.83 9.4–10.3 3	26.17 24.8–27.8 3
M. gallopavo merriami, Arizona	119.7 1	31.55 30.8–32.3 2	13.35 12.8–13.9 2	10.20 10.1–10.3 2	26.40 25.8–27.0 2
M. gallopavo Total skeletal specimens[c]	119.62 ± 4.13 111.2–129.8 30	31.23 ± 1.36 28.2–34.1 31	12.53 ± 0.60 11.5–13.9 31	9.56 ± 0.45 8.9–10.3 31	25.51 ± 1.03 22.9–27.8 31
M. californica Rancho La Brea	114.52 ± 3.10 106.4–121.4 31	28.83 ± 0.74 27.0–29.9 27	12.09 ± 0.55 10.7–13.4 30	9.31 ± 0.50 8.4–11.0 31	24.42 ± 0.54 23.4–25.4 26
M. californica Carpinteria	115.1 1	28.68 27.7–29.4 5	12.0 1	9.5 1	24.74 24.2–25.7 5
M. californica Total specimens	114.54 ± 3.05 106.4–121.4 32	28.81 ± 0.73 27.0–29.9 32	12.09 ± 0.54 10.7–13.4 31	9.32 ± 0.49 8.4–11.0 32	24.47 ± 0.56 23.4–25.7 31
Meleagris sp. Potter Creek Cave	116.9 1	31.9 1	~13.0 1	~9.9 1	26.2 1
M. ocellata Mayapán	110.40 108.8–112.0 2	27.42 26.1–28.5 6	11.33 11.0–12.0 3	8.73 7.9–9.2 3	22.94 ± 1.68 19.8–25.0 8
M. ocellata Yucatán, México and Petén, Guatemala	107.59 ± 2.03 104.2–110.7 10	27.68 ± 0.54 26.9–28.5 10	11.16 ± 0.29 10.8–11.6 10	8.94 ± 0.20 8.6–9.2 10	22.71 ± 0.78 21.7–24.1 10
M. crassipes San Josecito Cave	105.98 102.1–111.1 5	27.74 25.8–28.9 5	11.26 10.8–11.8 5	8.92 8.6–9.3 5	22.54 21.6–23.4 5

[a] From Howard 1963; [b] may possibly represent a male; [c] includes one specimen from northern Florida not identified to subspecies.

* Slightly damaged specimen.

Table 10. Measurements (in mm) of the ulna of male turkeys, with mean, standard deviation, observed range, and sample size. See Fig. 4 for explanation of measurements.

	Total Length	Proximal Width	Width of Midshaft	Depth of Midshaft	Distal Depth
Meleagris cf. *M. leopoldi* or *M. anza* Inglis IA	134.03* ± 2.85 128.0*–139.0* 15	18.14 ± 0.75 16.0–19.0 10	8.70 ± 0.34 8.1–9.1 32	9.70 ± 0.38 9.0–10.5 32	15.16 ± 0.65 14.3–16.1 12
Meleagris sp. Coleman IIA	137.40 133.4–139.4 5	19.15 18.7–19.8 6	8.98 ± 0.43 8.2–9.9 12	10.39 ± 0.38 9.9–11.0 11	15.95 ± 0.30 15.3–16.3 11
Meleagris sp. Sheffield Gravel Pits[a]	—	16.5* 1	—	—	14.7 1
M. gallopavo Manalapan	155.0* 153*–157* 2	20.00* 19.0*–21.0 2	9.57 9.0–10.0 3	10.63 10.3–10.9 3	16.05* 15.5*–16.6 2
Meleagris cf. *M. gallopavo* Sante Fe IIA	—	—	—	—	16.3* 1
Meleagris cf. *M. gallopavo* Reddick IB	—	19.3 1	9.5 1	10.9 1	—
M. gallopavo Ichetucknee River	141.50* 139.0*–144.0 2	19.77 19.0–20.3 3	9.30 8.9–9.6 3	10.73 10.5–10.9 3	16.45 16.0–16.9 2
M. gallopavo Seminole Field	—	—	—	—	16.30 16.1–16.4 3
Meleagris cf. *M. gallopavo* Haile IIA	—	—	10.4 1	12.0 1	—
Meleagris cf. *M. gallopavo* Mefford Cave I	150.0 1	20.0 1	10.0 1	11.2 1	17.4* 1
Meleagris sp. Santa Fe IVA	—	—	—	—	16.4* 1
M. gallopavo Good's Shellpit	—	—	9.0 1	10.2 1	15.8* 1
M. gallopavo Buffalo Site	152.33 150.0–157.0 3	20.18 ± 0.45 19.7–21.1 10	9.62 ± 0.42 9.0–10.7 45	10.90 ± 0.40 10.1–11.6 45	17.26 ± 0.68 16.3–18.8 16
M. gallopavo silvestris New York, Pennsylvania, Virginia	148.54 ± 3.63 143.0–158.0 24	19.72 ± 0.88 18.1–21.7 24	9.43 ± 0.62 8.0–10.4 23	11.00 ± 0.56 10.0–12.0 23	16.60 ± 0.57 15.2–17.9 23
M. gallopavo osceola, Florida	146.89 ± 5.75 139.8–156.0 8	18.89 ± 0.64 17.9–19.8 8	8.99 ± 0.49 8.2–9.8 8	10.15 ± 0.49 9.4–11.0 8	15.54 ± 0.54 14.9–16.3 8
M. gallopavo intermedia, Texas	157.0 1	20.5 1	10.2 1	10.6 1	16.3 1
M. gallopavo mexiana Chihuahua, México	150.0 1	19.3 1	10.0 1	11.2 1	17.9 1
M. gallopavo Total skeletal specimens	148.44 ± 4.36 139.8–158.0 34	19.53 ± 0.88 17.9–21.7 34	9.36 ± 0.62 8.0–10.4 33	10.79 ± 0.64 9.4–12.0 33	16.38 ± 0.75 14.9–17.9 33
M. californica Rancho La Brea	132.96 ± 3.81 124.6–139.0 36	18.14 ± 0.41 17.3–18.7 18	8.73 ± 0.25 7.9–9.3 36	9.89 ± 0.28 9.1–10.4 36	15.28 ± 0.54 14.5–16.3 22
M. californica Carpinteria	128.50 123.6–131.0 7	17.58 16.4–18.3 6	8.74 ± 0.30 8.1–9.1 9	9.82 ± 0.13 9.7–10.1 9	15.14 ± 0.63 14.3–16.2 8
M. californica Total specimens	132.23 ± 3.98 123.6–139.0 43	18.00 ± 0.54 16.4–18.7 24	8.73 ± 0.26 7.9–9.3 45	9.88 ± 0.26 9.1–10.4 45	15.24 ± 0.56 14.3–16.3 30
M. ocellata Dzibilchaltún	136.0 1	17.10* 16.2–18.0* 2	7.95 7.3–8.6 2	9.60 9.2–10.0 2	15.3 1

Continued

Table 10. Continued.

	Total Length	Proximal Width	Width of Midshaft	Depth of Midshaft	Distal Depth
Meleagris cf. *M. ocellata,* Tulúm	127.0* 1	—	—	—	—
M. ocellata Yucatán, México and Petén, Guatemala	125.70 ± 3.22 120.5–130.5 8	16.32 ± 1.29 14.0–17.8 8	7.31 ± 0.31 6.8–7.7 8	8.98 ± 0.63 7.7–9.6 8	13.50 ± 1.21 11.6–15.3 8
M. crassipes San Josecito Cave	113.95 112.9–115.0 2	16.0* 1	7.40 7.3–7.5 3	8.47 8.2–8.7 3	13.05* 13.0–13.1* 2

[a] May possibly represent a female.

* Slightly damaged specimen.

Table 11. Measurements (in mm) of the ulna of female turkeys, with mean, standard deviation, observed range, and sample size. See Fig. 4 for explanation of measurements.

	Total Length	Proximal Width	Width of Midshaft	Depth of Midshaft	Distal Depth
Meleagris cf. *M. leopoldi* or *M. anza* Inglis IA	107.75* 103.0*–112.5* 2	15.47 15.4–15.6 3	7.38 7.1–8.1 6	8.24 7.9–8.9 6	12.90 12.2–13.6 4
Meleagris sp. Coleman IIA	121.0 1	15.47 15.3–15.8 3	7.57 7.3–8.0 3	8.78 8.2–9.3 4	13.38* 13.0–13.7* 4
Meleagris sp. Howell's Ridge Cave	—	13.4** 1	—	—	12.2* 1
M. gallopavo Ichetucknee River	118.90 118.2–119.6 2	—	8.9 1	8.70 8.7 2	13.7 1
M. gallopavo Seminole Field	—	14.83* 14.5*–15.1 3	—	—	12.9* 1
M. gallopavo Nichol's Hammock	112.08 107.7–115.1 4	14.38 13.3–15.0 5	6.88 6.4–7.1 4	7.68 7.3–7.9 4	12.10 11.9–12.3 4
M. gallopavo Good's Shellpit	108.6 1	13.9 1	7.0 1	8.0 1	11.3 1
M. gallopavo Buffalo Site	122.50 ± 3.37 116.0–127.0 12	16.39 ± 0.38 15.8–17.2 10	7.75 ± 0.30 7.0–8.2 52	8.76 ± 0.34 8.0–9.5 52	13.86 ± 0.37 13.1–14.5 17
M. gallopavo silvestris, New York, Pennsylvania, Virginia	118.71 ± 3.32 112.9–123.0 12	15.45 ± 0.42 15.0–16.2 13	7.14 ± 0.33 6.8–7.9 12	8.39 ± 0.37 8.0–9.0 12	13.21 ± 0.36 12.9–14.0 12
M. gallopavo osceola, Florida	113.62 ± 3.29 109.8–120.2 11	14.99 ± 0.62 13.9–16.1 11	7.06 ± 0.17 6.7–7.2 11	7.84 ± 0.28 7.3–8.2 11	12.45 ± 0.36 11.9–12.8 11
M. gallopavo mexicana Chihuahua, México	123.25 119.1–127.4 2	16.80 16.1–17.5 2	7.75 7.3–8.2 2	8.75 8.4–9.1 2	14.25 14.0–14.5 2
M. gallopavo merriami, Arizona	125.5 1	18.1 1	7.5 1	9.1 1	14.0 1
M. gallopavo Total skeletal specimens[a]	116.82 ± 5.04 107.8–127.4 27	15.45 ± 0.86 13.9–18.1 28	7.16 ± 0.34 6.7–8.2 27	8.18 ± 0.50 7.3–9.1 27	12.95 ± 0.69 11.7–14.5 27
M. californica Rancho La Brea	108.95 ± 2.98 102.7–115.5 21	14.37 ± 0.42 13.6–15.1 17	6.98 ± 0.31 6.2–7.4 21	8.03 ± 0.27 7.6–8.6 21	12.24 ± 0.36 11.7–13.0 16
M. californica Carpinteria	110.92 108.1–115.8 4	14.98 14.6–15.6 4	7.08 6.9–7.4 7	8.21 8.0–8.4 7	12.61 ± 0.40 12.1–13.4 8
M. californica Total specimens	109.26 ± 3.06 102.7–115.8 25	14.48 ± 0.48 13.6–15.6 21	7.01 ± 0.28 6.2–7.4 28	8.08 ± 0.26 7.6–8.6 28	12.36 ± 0.41 11.7–13.4 24
M. ocellata Yucatán, México and Petén, Guatemala	108.39 ± 2.20 104.1–112.1 10	13.82 ± 0.73 12.8–15.0 10	6.40 ± 0.38 5.8–6.8 10	7.88 ± 0.35 7.3–8.3 10	11.78 ± 0.37 11.1–12.3 10
M. crassipes San Josecito Cave	106.35 106.0–106.7 2	13.5* 1	6.50 5.9–6.8 6	7.53 7.4–7.8 6	11.63 11.3–11.9 3

[a] Includes one specimen from northern Florida not identified to subspecies.

* Slightly damaged specimen.

** Moderately damaged specimen.

Table 12. Measurements (in mm) of the radius of male turkeys, with mean, standard deviation, observed range, and sample size. See Fig. 4 for explanation of measurements.

	Total Length	Proximal Width	Proximal Depth	Least Width of Shaft	Least Depth of Shaft	Distal Width
Meleagris cf. *M. leopoldi* or *M. anza* Inglis IA	119.93* 117.8*–121.5* 3	9.47 9.1–10.2 6	10.64 ± 0.58 9.7–11.7 10	5.02 ± 0.18 4.6–5.3 13	4.61 ± 0.28 3.9–4.9 14	12.72 ± 0.51 11.8–13.7 11
Meleagris sp. Coleman IIA	120.55 119.3–121.8 2	10.12 9.8–10.4 4	11.02 10.3–11.5 4	5.48 5.1–5.7 4	4.40 4.0–5.0 3	13.40 12.9–13.9 2
M. gallopavo Manalapan	142* 1	—	—	—	—	—
Meleagris cf. *M. gallopavo* Rock Spring	—	10.3 1	—	—	4.2 1	13.1 1
Meleagris cf. *M. gallopavo* Reddick IB	—	—	—	—	4.7 1	13.1 1
M. gallopavo Aucilla River	135.5* 1	—	—	5.3 1	4.2 1	—
M. gallopavo Ichetucknee River	137.0 1	11.4 1	12.1 1	5.9 1	4.9 1	15.0 1
Meleagris sp. Florida Lime Co.	—	—	—	—	5.0 1	13.1* 1
Meleagris cf. *M. gallopavo* Mefford Cave I	133.5 1	11.0 1	12.9 1	6.0 1	5.0 1	14.9 1
Meleagris cf. *M. gallopavo* Steinhatchie River	137.0 1	11.0* 1	11.0* 1	6.4 1	5.6 1	13.9* 1
M. gallopavo Nichol's Hammock	—	—	—	5.1 1	4.6 1	13.9 1
M. gallopavo Buffalo Site	138.25 136.0–140.0 4	11.51 ± 0.55 10.8–12.3 15	12.15 ± 0.40 11.1–12.8 17	5.66 ± 0.31 5.2–6.2 21	4.82 ± 0.22 4.4–5.2 25	14.42 ± 0.34 14.0–15.0 13
M. gallopavo silvestris, New York, Pennsylvania, Virginia	134.60 ± 4.32 127.0–145.0 24	10.90 ± 0.53 9.8–11.8 23	11.83 ± 0.49 10.7–12.7 23	5.57 ± 0.38 5.0–6.4 23	4.72 ± 0.30 4.0–5.1 23	13.77 ± 0.44 12.8–15.0 23
M. gallopavo osceola, Florida	132.94 ± 5.00 126.7–141.9 9	9.98 ± 0.57 9.3–10.9 9	10.79 ± 0.36 10.2–11.2 9	5.14 ± 0.16 4.9–5.5 9	4.32 ± 0.24 4.0–4.7 9	12.94 ± 0.37 12.3–13.4 9
M. gallopavo intermedia, Texas	142.0 1	11.7 1	11.7 1	5.6 1	—	13.6 1
M. gallopavo Total skeletal specimens	134.38 ± 4.63 126.7–145.0 34	10.67 ± 0.69 9.3–11.8 33	11.54 ± 0.65 10.2–12.7 33	5.45 ± 0.38 4.9–6.4 33	4.61 ± 0.34 4.0–5.1 32	13.54 ± 0.55 12.3–15.0 33
M. californica Rancho La Brea	117.66 ± 2.62 111.5–121.6 22	9.46 ± 0.42 8.7–10.4 28	10.58 ± 0.45 9.9–11.8 28	4.99 ± 0.24 4.6–5.6 21	4.43 ± 0.21 4.0–4.9 35	12.55 ± 0.39 11.9–13.3 30
M. californica Carpinteria	115.98 113.8–119.1 4	9.49 ± 0.33 8.9–10.0 8	10.62 ± 0.50 9.8–11.3 8	5.12 5.0–5.4 5	4.60 4.2–4.9 6	12.43 12.1–12.8 6
M. californica Total specimens	117.40 ± 2.60 111.5–121.6 26	9.47 ± 0.40 8.7–10.4 36	10.59 ± 0.46 9.8–11.3 36	5.02 ± 0.23 4.6–5.6 26	4.45 ± 0.23 4.0–4.9 41	12.53 ± 0.37 11.9–13.3 36
Meleagris cf. *M. californica* La Mirada	120.5 1	9.9 1	10.6 1	4.9 1	4.1 1	12.3 1
Meleagris sp. Imperial Highway	—	—	—	—	—	12.6* 1
M. ocellata Yucatán, México and Petén, Guatemala	112.70 ± 2.67 108.1–117.0 8	9.00 ± 0.94 7.3–10.1 8	9.54 ± 0.73 8.6–10.6 8	4.38 ± 0.52 3.4–4.9 8	3.69 ± 0.48 2.9–4.2 8	11.21 ± 1.32 9.1–13.0 8
M. crassipes San Josecito Cave	97.8* 1	8.9 1	—	4.7 1	4.1 1	11.2* 1

* Slightly damaged specimen.

Table 13. Measurements (in mm) of the radius of female turkeys, with mean, standard deviation, observed range, and sample size. See Fig. 4 for explanation of measurements.

	Total Length	Proximal Width	Proximal Depth	Least Width of Shaft	Least Depth of Shaft	Distal Width
Meleagris cf. *M. leopoldi* or *M. anza* Inglis IA	100.9 1	7.70 7.2–8.2 2	8.2 1	3.94 3.7–4.2 5	3.55 3.3–3.8 4	10.35 10.2–10.5 2
Meleagris sp. Coleman IIA	—	—	—	—	4.0 1	11.1 1
Meleagris cf. *M. gallopavo* Rock Spring	—	—	—	—	3.6 1	—
M. gallopavo Buffalo Site	111.60 ± 3.20 107.0–117.0 10	8.88 ± 0.38 8.1–9.5 16	9.81 ± 0.41 9.1–10.7 16	4.55 ± 0.28 4.1–5.1 13	3.94 ± 0.20 3.7–4.6 18	11.88 ± 0.34 11.4–12.9 16
M. gallopavo silvestris, New York, Pennsylvania, Virginia	107.70 ± 3.17 102.0–112.7 12	8.61 ± 0.32 8.2–9.2 13	9.23 ± 0.26 8.9–9.8 13	4.22 ± 0.25 3.9–4.7 12	3.65 ± 0.27 3.2–4.0 12	11.04 ± 0.40 10.3–11.8 12
M. gallopavo osceola, Florida	102.89 ± 3.13 99.2–108.6 11	7.84 ± 0.41 7.2–8.6 11	8.34 ± 0.40 7.8–9.1 11	4.07 ± 0.20 3.8–4.4 11	3.38 ± 0.23 3.1–3.7 11	10.52 ± 0.41 9.9–11.1 11
M. gallopavo mexicana Chihuahua, México	111.30 108.1–114.5 2	9.00 8.1–9.9 2	9.70 9.5–9.9 2	4.20 4.1–4.3 2	3.95 3.7–4.2 2	11.55 11.2–11.9 2
M. gallopavo merriami, Arizona	112.3 1	8.9 1	10.4 1	4.5 1	3.7 1	12.1 1
M. gallopavo Total skeletal specimens[a]	106.14 ± 4.23 99.2–114.5 27	8.32 ± 0.59 7.2–9.9 28	8.91 ± 0.66 7.8–10.4 28	4.16 ± 0.23 3.8–4.7 27	3.54 ± 0.31 3.1–4.2 27	10.87 ± 0.57 9.9–12.1 27
M. californica Rancho La Brea	97.72 ± 2.60 93.8–104.9 13	7.74 ± 0.38 7.1–8.4 18	8.51 ± 0.38 8.0–9.2 15	4.13 ± 0.20 3.9–4.5 13	3.59 ± 0.20 3.3–4.0 20	10.41 ± 0.30 9.8–10.8 17
M. californica Carpinteria	96.05 95.3–96.8 2	8.28 7.9–8.5 4	8.62 8.1–9.1 4	4.07 3.9–4.4 3	3.72 3.5–4.0 4	10.50 10.3–10.9 4
M. californica Total specimens	97.50 ± 2.50 93.8–104.9 15	7.84 ± 0.42 7.1–8.5 22	8.53 ± 0.40 8.0–9.2 19	4.12 ± 0.21 3.9–4.5 16	3.61 ± 0.21 3.3–4.0 24	10.43 ± 0.29 9.8–10.9 21
M. ocellata Yucatán, México and Petén, Guatemala	97.20 ± 2.35 92.8–100.7 10	7.66 ± 0.40 7.1–8.3 10	8.10 ± 0.30 7.7–8.8 10	3.80 ± 0.27 3.5–4.1 10	3.27 ± 0.24 2.9–3.7 10	9.83 ± 0.58 9.2–11.0 10
M. crassipes San Josecito Cave	—	—	—	4.0 1	3.5 1	—

[a] Includes one specimen from Florida not identified to subspecies.

Table 14. Measurements (in mm) of the carpometacarpus of male turkeys, with mean, standard deviation, observed range, and sample size. See Fig. 5 for explanation of measurements.

	Total Length	Proximal Depth	Length of Metacarpal I	Least Width of Metacarpal II	Least Depth of Metacarpal II	Greatest Depth of Intermetacarpal Space	Distal Depth	Protrusion of Metacarpal III beyond Knob of Metacarpal II
Meleagris progenes Rexroad	66.6[a] 1	20.0[a] 1	10.0 1	80[a] 1	5.7 1	8.0* 1	17.2 1	3.8[a] 1
Meleagris cf. *M. leopoldi* or *M. anza*, Inglis IA	72.63 ± 1.86 69.5–76.3 15	20.72 ± 0.64 19.6–22.0 10	10.80 ± 0.54 9.7–11.8 17	8.41 ± 0.43 7.8–9.4 27	6.26 ± 0.29 5.3–6.9 27	7.18 ± 0.47 6.4–8.0 13	18.68 ± 0.86 17.3–20.1 12	3.30 ± 0.40 2.8–4.0 17
Meleagridinae, cf. *Meleagris*, Port Kennedy Cave	73.6 1	19.6 1	12.2 1	—	6.8 1	—	18.0 1	4.1 1
Meleagris sp. Coleman IIA	75.64 73.6–77.0 5	22.00 21.4–22.8 6	11.00 10.3–11.6 6	8.55 8.2–8.9 6	6.28 5.9–6.9 6	7.48 7.0–8.5 4	19.80 18.6–20.8 3	3.50 3.1–3.9 6
Meleagris cf. *M. gallopavo* Rock Spring	—	—	—	8.0 1	6.55 6.3–6.8 2	—	—	3.80 3.6–4.0 2
Meleagris cf. *M. gallopavo* Reddick IB	76.7 1	22.7 1	—	8.5 1	6.4 1	—	—	3.57 3.3–4.0 3
Meleagris cf. *M. gallopavo* Melbourne	79.0 1	21.85* 21.8*–21.9* 2	11.60 11.3–11.9 2	8.20 8.2 2	6.0 1	—	—	3.9 1
M. gallopavo Ichetucknee River	78.28 ± 2.40 74.0–82.1 8	23.00 21.9–24.9 5	11.98 ± 0.44 11.3–12.7 8	8.90 ± 0.58 8.2–10.0 8	6.59 ± 0.47 6.1–7.9 9	8.28 7.8–9.1 5	21.05* 20.3–22.6* 4	3.83 3.4–4.3 7
M. gallopavo Seminole Field	—	—	11.4 1	9.25 9.1–9.4 2	6.65 6.3–7.0 2	—	—	4.03 3.8–4.5 3
Meleagris sp. Florida Lime Co.	—	—	—	8.2 1	5.90 5.8–6.0 2	—	—	3.35 3.1–3.6 2
Meleagris cf. *M. gallopavo* Mefford Cave I	83.6 1	—	13.0 1	9.5 1	6.5 1	8.1 1	21.5 1	3.8 1
M. gallopavo Nichol's Hammock	—	21.8 1	12.7 1	—	—	—	—	—
M. gallopavo Good's Shellpit	77.1 1	—	—	7.4 1	6.1 1	—	—	3.1 1
M. gallopavo Buffalo Site	82.80 ± 2.13 79.0–89.5 59	24.36 ± 0.71 22.7–26.1 61	12.31 ± 0.60 10.8–13.8 52	8.98 ± 0.54 7.5–10.1 115	6.80 ± 0.35 5.9–7.8 120	8.22 ± 0.55 6.5–9.5 65	21.56 ± 0.68 19.8–23.1 34	3.99 ± 0.41 3.0–4.9 66
M. gallopavo Hartman's Cave	—	—	—	8.3 1	6.6 1	8.5 1	—	—
M. gallopavo silvestris, New York, Pennsylvania, Virginia	80.29 ± 2.22 76.1–83.7 26	23.60 ± 0.88 21.9–25.2 26	11.85 ± 0.48 11.0–13.1 26	8.97 ± 0.71 7.6–10.2 26	6.34 ± 0.48 5.7–7.5 26	8.00 ± 0.70 6.5–9.3 25	20.64 ± 0.74 18.9–22.1 26	4.24 ± 0.49 3.3–5.7 25
M. gallopavo osceola, Florida	79.60 ± 3.00 74.3–84.2 9	22.18 ± 0.78 20.6–23.2 9	11.68 ± 0.38 11.0–12.2 9	8.14 ± 0.32 7.6–8.6 9	6.41 ± 0.46 5.9–7.0 9	7.51 ± 0.42 7.0–8.2 9	19.41 ± 0.79 18.4–20.9 9	3.62 ± 0.37 3.1–4.1 9
M. gallopavo intermedia, Texas	84.0 1	23.1 1	14.5 1	9.0 1	6.6 1	7.4 1	19.7 1	4.2 1
M. gallopavo Total skeletal specimens	80.22 ± 2.46 74.3–84.2 36	23.23 ± 1.04 20.6–25.2 36	11.88 ± 0.64 11.0–14.5 36	8.77 ± 0.72 7.6–10.2 36	6.36 ± 0.47 5.7–7.5 36	7.86 ± 0.66 6.5–9.3 35	20.30 ± 0.92 18.4–22.1 36	4.08 ± 0.53 3.1–5.7 35

Table 14. Continued.

	Total Length	Proximal Depth	Length of Metacarpal I	Least Width of Metacarpal II	Least Depth of Metacarpal II	Greatest Depth of Intermetacarpal Space	Distal Depth	Protrusion of Metacarpal III beyond Knob of Metacarpal II
M. californica Rancho La Brea	72.62 ± 2.03 67.5–77.1 32	20.58 ± 0.66 19.4–21.9 31	11.28 ± 0.56 10.3–12.2 32	8.11 ± 0.54 7.1–9.0 32	6.25 ± 0.32 5.6–7.1 32	7.45 ± 0.50 6.5–8.4 32	19.19 ± 0.63 17.9–20.4 23	3.38 ± 0.38 2.3–4.1 32
M. californica Carpinteria	73.80 71.3–76.7 3	20.76 20.2–21.4 5	11.36 10.5–12.4 5	8.33 7.9–8.8 3	6.32 6.1–6.4 5	7.50 7.2–7.8 3	19.25 19.0–19.5 2	3.33 3.1–3.6 6
M. californica Total specimens	72.72 ± 2.08 67.5–77.1 35	20.60 ± 0.64 19.4–21.9 36	11.29 ± 0.56 10.3–12.4 37	8.13 ± 0.53 7.1–9.0 35	6.26 ± 0.30 5.6–7.1 37	7.45 ± 0.48 6.5–8.4 35	19.19 ± 0.60 17.9–20.4 25	3.37 ± 0.35 2.3–4.1 38
M. ocellata Dzibilchaltún	67.47 66.7–68.2 3	20.15 20.0–20.3 2	10.43 10.1–11.0 3	7.13 6.6–7.8 3	5.12 4.7–5.6 4	6.80 6.6–7.1 3	17.3 1	2.88 2.5–3.1 4
Meleagris cf. *M. ocellata*, Macanché	—	—	—	—	5.4 1	—	—	—
M. ocellata Mayapán	68.03 ± 2.63 62.2–72.1 23	20.27 ± 0.54 19.5–21.3 10	10.80 ± 0.65 9.3–11.8 19	7.17 ± 0.64 6.1–8.2 18	5.42 ± 0.34 4.9–5.9 17	7.07 ± 0.52 6.5–8.0 12	18.8 1	3.22 ± 0.31 2.8–3.9 18
M. ocellata Yucatán, México and Petén, Guatemala	66.42 ± 2.37 63.3–69.4 9	19.79 ± 0.96 18.8–21.2 9	10.51 ± 0.56 10.0–11.6 9	7.40 ± 0.62 6.0–8.1 9	5.27 ± 0.46 4.5–5.9 9	6.68 6.0–7.2 7	16.86 ± 1.30 15.1–18.8 9	3.10 2.2–3.8 7
M. crassipes San Josecito Cave	59.60 58.8–60.4 2	18.30* 18.2–18.4* 2	9.25 9.1–9.4 2	7.30 7.1–7.5 2	4.75 4.6–4.9 2	6.60 6.3–6.9 2	16.8 2	3.35 3.3–3.4 2

[a] From Brodkorb 1964b.

* Slightly damaged specimen.

Table 15. Measurements (in mm) of the carpometacarpus of female turkeys, with mean, standard deviation, observed range, and sample size. See Fig. 5 for explanation of measurements.

	Total Length	Proximal Depth	Length of Metacarpal I	Least Width of Metacarpal II	Least Depth of Metacarpal II	Greatest Depth of Intermetacarpal Space	Distal Depth	Protrusion of Metacarpal III beyond Knob of Metacarpal II
Meleagris progenes Rexroad	—	—	—	6.05 5.8–6.3[a] 2	—	—	—	2.7 1
Meleagris cf. *M. leopoldi* or *M. anza*, Inglis IA	61.25 ± 1.71 58.3–63.1 8	17.80 17.7–17.9 2	9.48 9.1–9.9 6	6.48 ± 0.38 6.2–7.6 11	5.22 ± 0.20 4.9–5.6 12	5.96 5.6–6.6 7	15.40 14.8–16.0 5	2.46 2.0–3.2 7
Meleagris sp. Coleman IIA	—	18.03 17.5–18.3 3	9.87 9.3–10.2 3	7.0 1	5.6 1	—	—	—
Meleagris cf. *M. gallopavo* Burnet Cave[b]	63.3 1	—	—	7.5 1	5.2 1	6.3 1	—	3.1 1
Meleagris sp. Haile VIIA	—	—	—	7.4 1	6.0 1	—	—	—
Meleagris cf. *M. gallopavo* Reddick IB	—	—	—	—	5.5 1	—	—	3.2 1
Meleagris cf. *M. gallopavo* Melbourne	61.3* 1	—	—	6.9 1	4.8 1	—	—	—
M. gallopavo Ichetucknee River	66.8 1	18.9* 1	9.9 1	7.1 1	5.2 1	6.8 1	16.0* 1	2.4 1
Meleagris cf. *M. gallopavo*, Vero	60.0 1	—	—	6.2 1	4.7 1	—	—	3.2 1
M. gallopavo Seminole Field	—	18.7 1	9.6 1	7.3 1	5.10 5.1 2	—	—	2.82 2.3–3.1 4
M. gallopavo Nichol's Hammock	61.60 60.3–62.9 2	17.20 17.1–17.3 2	9.05 8.3–9.8 2	7.00 6.8–7.2 2	4.85 4.8–4.9 2	6.4 1	—	2.70 2.5–2.9 2
M. gallopavo Good's Shellpit	62.1 1	17.9 1	10.0 1	7.0 1	4.9 1	—	—	2.2 1
M. gallopavo Buffalo Site	67.68 ± 1.82 63.7–72.7 67	19.50 ± 0.58 17.6–20.9 76	10.36 ± 0.47 9.3–11.5 79	7.25 ± 0.40 6.2–8.2 145	5.29 ± 0.30 4.5–6.2 149	7.00 ± 0.45 6.0–8.0 88	17.68 ± 0.67 16.1–19.0 38	3.16 ± 0.38 2.2–4.4 94
M. gallopavo silvestris, New York, Pennsylvania, Virginia	65.48 ± 1.30 63.0–68.2 14	19.21 ± 0.52 18.5–20.1 14	10.06 ± 0.32 9.7–10.9 14	6.94 ± 0.34 6.3–7.8 14	4.74 ± 0.26 4.3–5.2 14	6.76 ± 0.42 6.1–7.5 14	16.87 ± 0.62 15.8–18.0 14	3.23 ± 0.35 2.8–3.9 14
M. gallopavo osceola, Florida	63.16 ± 2.75 59.7–67.8 11	17.54 ± 0.72 16.7–19.1 11	9.40 ± 0.55 8.7–10.4 11	6.44 ± 0.25 6.1–6.8 11	4.82 ± 0.13 4.6–5.1 11	6.05 ± 0.44 5.4–6.9 11	15.52 ± 0.67 14.4–16.5 11	2.76 ± 0.41 2.3–3.6 11
M. gallopavo mexicana Chihuahua, México	68.45 66.5–70.4 2	19.40 19.2–19.6 2	10.35 10.2–10.5 2	7.10 6.8–7.4 2	5.30 5.3 2	6.75 6.5–7.0 2	16.95 16.6–17.3 2	3.75 3.3–4.2 2
M. gallopavo[c] Total skeletal specimens	64.60 ± 2.64 59.5–70.4 28	18.51 ± 1.02 16.7–20.1 28	9.76 ± 0.60 8.4–10.9 28	6.73 ± 0.41 6.1–7.8 28	4.81 ± 0.24 4.3–5.2 28	6.45 ± 0.55 5.4–7.5 28	16.27 ± 0.95 14.4–18.0 28	3.07 ± 0.47 2.3–4.2 28
M. californica Rancho La Brea	61.46 ± 1.37 59.1–65.5 32	17.34 ± 0.39 16.6–18.2 32	9.83 ± 0.30 9.2–10.4 31	6.68 ± 0.40 6.0–7.5 32	5.18 ± 0.30 4.6–5.9 32	6.60 ± 0.23 6.2–7.0 32	16.48 ± 0.46 15.5–17.2 23	2.68 ± 0.25 2.2–3.2 32

Table 15. Continued.

	Total Length	Proximal Depth	Length of Metacarpal I	Least Width of Metacarpal II	Least Depth of Metacarpal II	Greatest Depth of Intermetacarpal Space	Distal Depth	Protrusion of Metacarpal III beyond Knob of Metacarpal II
M. californica	61.70	17.80	9.99 ± 0.46	7.07	5.01	6.42	16.58	2.73
Carpinteria	60.8–62.6	17.3–18.7	9.4–10.9	6.1–7.8	4.8–5.3	6.1–6.8	16.3–17.3	2.5–3.1
	6	7	8	6	7	5	5	7
M. californica	61.50 ± 1.27	17.42 ± 0.45	9.86 ± 0.34	6.74 ± 0.45	5.15 ± 0.28	6.58 ± 0.25	16.50 ± 0.45	2.68 ± 0.24
Total specimens	59.1–65.5	16.6–18.7	9.2–10.9	6.0–7.8	4.6–5.9	6.1–7.0	15.5–17.3	2.2–3.2
	38	39	39	38	39	37	28	39
Meleagris cf. *M.*	56.8*	—	—	5.2	3.8	5.8	13.7	3.1
ocellata, Tulúm	1			1	1	1	1	1
M. ocellata	53.92	17.2	8.40	5.60	4.07	5.73	15.2	2.80
Mayapán	49.3–59.4		8.0–8.8	5.1–6.0	3.8–4.2	5.1–6.9		2.7–2.9
	4	1	2	3	3	3	1	2
M. ocellata	57.60 ± 1.27	17.09 ± 0.46	9.12 ± 0.62	6.38 ± 0.27	4.79 ± 0.18	6.02 ± 0.44	14.97 ± 0.60	2.54 ± 0.30
Yucatán, México	56.2–60.1	16.6–18.0	8.3–10.6	5.9–6.7	4.4–5.0	5.6–6.9	13.9–16.0	2.0–2.9
and Petén,	10	10	10	10	10	8	10	8
Guatemala								
M. crassipes	56.16*	16.03*	9.13*	6.70	4.48 ± 0.16	6.26	15.75	2.38
San Josecito	54.4*–57.2	15.7–16.7*	8.6–9.7*	6.6–6.8	4.3–4.8	6.0–6.7	15.7–15.8	2.2–2.6
Cave[d]	7	3	3	5	8	5	2	7

[a] From Brodkorb 1964b; [b] may represent a male; [c] includes one specimen from northern Florida not identified to subspecies; [d] may possibly include one or more specimens which represent males.

* Slightly damaged specimen.

Table 16. Measurements (in mm) of the femur of male turkeys, with mean, standard deviation, observed range, and sample size. See Fig. 5 for explanation of measurements.

	Total Length	Proximal Width	Depth of Head	Width of Midshaft	Depth of Midshaft	Distal Width	Depth of Internal Condyle	Depth of External Condyle	Depth of Fibular Condyle
Meleagris progenes[a] Rexroad	—	25.8* 1	—	—	—	—	—	—	—
Meleagris sp. University Drive	—	—	—	—	—	26.7* 1	—	22.2 1	19.9 1
Meleagris cf. *M. leopoldi* or *M. anza*, Inglis IA	123.21* ± 2.57 118.8*–127.0* 16	29.96 ± 0.83 29.0–31.2 14	11.29 ± 0.41 10.7–12.1 13	12.23 ± 0.50 11.2–13.3 34	10.90 ± 0.51 10.2–11.9 34	26.95 25.5–27.9 6	22.16* ± 0.82 20.2*–23.3* 14	22.55 ± 0.94 21.3–24.6 13	19.78 ± 0.86 18.7–21.1 11
Meleagris sp. Williston	130.0* 1	31.2 1	11.3 1	12.7 1	10.9 1	—	—	22.8 1	20.7 1
Meleagris sp. Coleman IIA	131.24* 129.1*–133.0 5	33.03* 32.4–34.0* 7	12.46 ± 0.41 11.8–13.2 9	12.83 ± 0.56 12.1–13.8 14	11.56 ± 0.52 10.5–12.2 14	28.70 28.2–29.4 5	23.56* 22.3*–24.7* 5	23.50 22.4–24.8 7	20.47 19.6–21.7 6
Meleagris cf. *M. gallopavo* Frankstown Cave	—	—	12.9 1	—	—	—	—	—	—
M. gallopavo Manalapan	147.50 145.0–150.0[b] 2	32.6 1	13.17 13.0–13.3 3	13.60 13.2–13.9 3	12.53 12.1–13.0 3	30.1 1	25.2 1	25.1 1	21.2* 1
Meleagris cf. *M. gallopavo*, Santa Fe River IIA	133.2* 1	32.7 1	12.2 1	13.1 1	11.7 1	29.6 1	—	24.3 1	21.5 1
Meleagris cf. *M. gallopavo* Reddick IB	138.5* 1	33.7 1	12.3 1	14.0 1	11.4 1	30.55* 30.3–30.8* 2	24.50 24.0–25.0 2	25.0 24.8–25.2 2	22.8 1
M. gallopavo Ichetucknee River	141.75* 139.7*–143.8* 2	36.05 36.0–36.1 2	13.15 13.1–13.2 2	14.07 13.3–14.6 3	12.43 11.4–13.0 3	30.75* 30.1*–31.4* 2	25.2* 1	23.88* 21.0*–25.6* 4	20.65* 18.2*–21.8* 4
M. gallopavo Seminole Field	—	—	—	12.90 12.6–13.2 2	11.05 10.3–11.8 2	28.9* 1	25.5* 1	—	—
M. gallopavo Davis Quarry	—	33.5 1	12.2 1	—	—	—	—	—	—
Meleagris sp. St. Mark's River	—	31.7* 1	10.3* 1	—	—	—	—	—	—
M. gallopavo Good's Shellpit	124.60* 124.5*–124.7* 2	—	10.5 1	12.15 12.1–12.2 2	10.70 10.4–11.0 2	26.55 26.4–26.7 2	22.80 22.0–23.6 2	21.60 20.5–22.9 3	19.15 18.9–19.4 2
Meleagris sp. Silver Glen Springs	—	—	—	—	—	25.5 1	23.2* 1	22.1 1	19.0 1
M. gallopavo Buffalo Site	142.0 1	35.37 32.5–36.9 7	12.91 ± 0.40 12.1–13.5 11	13.59 ± 0.70 12.0–15.1 15	11.91 ± 0.55 11.2–13.4 15	30.93 29.7–31.6 3	—	24.28 23.4–25.3 4	21.45 20.0–22.7 4

Table 16. Continued.

	Total Length	Proximal Width	Depth of Head	Width of Midshaft	Depth of Midshaft	Distal Width	Depth of Internal Condyle	Depth of External Condyle	Depth of Fibular Condyle
M. gallopavo silvestris, New York, Pennsylvania, Virginia	139.30 ± 4.37 127.0–150.0 28	34.65 ± 1.20 32.6–37.1 28	12.79 ± 0.37 12.0–13.4 27	13.60 ± 0.77 12.0–15.2 28	11.99 ± 0.64 10.9–13.3 28	29.91 ± 0.85 27.9–32.0 28	24.65 ± 0.85 23.1–26.0 27	24.21 ± 0.79 22.6–25.5 27	21.06 ± 0.78 19.7–22.5 27
M. gallopavo osceola, Florida	135.99 ± 5.32 128.7–146.7 9	32.59 ± 1.59 30.8–34.9 9	11.59 ± 0.49 10.7–12.2 9	13.38 ± 0.58 12.2–14.1 9	11.07 ± 0.53 10.0–11.8 9	27.76 ± 0.84 26.0–29.3 9	23.73 ± 1.20 21.6–25.4 9	23.06 ± 0.96 21.4–24.8 9	20.17 ± 0.92 19.0–21.8 9
M. gallopavo intermedia, Texas	144.0 1	—	—	13.5 1	11.5 1	27.2 1	—	—	20.1 1
M. gallopavo mexicana, Chihuahua, México	145.0 1	35.6 1	12.6 1	14.8 1	12.9 1	31.1 1	25.4 1	24.7 1	22.3 1
M. gallopavo merriami Arizona	143.0 1	33.8 1	12.8 1	14.4 1	12.3 1	29.6 1	24.5 1	24.2 1	21.2 1
M. gallopavo Total skeletal specimens	138.91 ± 4.81 127.0–150.0 40	34.18 ± 1.54 30.8–37.1 39	12.50 ± 0.64 10.7–13.4 38	13.60 ± 0.74 12.0–15.2 40	11.80 ± 0.73 10.0–13.3 40	29.38 ± 1.29 26.0–32.0 40	24.45 ± 1.00 21.6–26.0 38	23.93 ± 0.98 21.4–25.5 38	20.87 ± 0.90 19.0–22.5 39
M. californica Rancho La Brea	124.19* ± 3.08 117.7*–132.2* 35	31.47 ± 1.25 28.6–33.8 44	11.45 ± 0.50 10.4–12.6 48	12.18 ± 0.45 11.4–13.2 43	10.25 ± 0.43 8.9–11.1 43	27.82 ± 0.85 25.8–29.3 34	22.28 ± 0.88 21.1–23.7 10	22.21 ± 0.87 20.0–23.7 26	19.95 ± 0.97 18.1–21.8 33
M. californica Carpinteria	127.20* 124.7*–128.8* 3	31.70 31.4–32.0 3	11.40 11.2–11.7 5	12.38 11.8–13.1 6	10.57 10.2–10.9 6	27.80 27.1–28.2 3	22.2 1	22.43 22.0–22.9 3	19.83 18.8–20.4 3
M. californica Total specimens	124.43* ± 3.11 117.7*–132.2* 38	31.48 ± 1.21 28.6–33.8 47	11.44 ± 0.47 10.4–12.6 53	12.20 ± 0.45 11.4–13.2 49	10.29 ± 0.43 8.9–11.1 49	27.82 ± 0.82 25.8–29.3 37	22.27 ± 0.83 21.1–23.7 11	22.23 ± 0.84 20.0–23.7 29	19.94 ± 0.96 18.1–21.8 36
M. ocellata Yucatán, México, and Petén, Guatemala	110.84 ± 3.37 105.6–116.9 10	25.96 ± 1.15 24.1–27.8 10	9.36 ± 0.44 8.9–10.2 8	10.40 ± 0.66 9.3–11.7 10	9.49 ± 0.66 8.3–10.2 10	23.63 ± 1.05 22.1–25.2 10	19.04 ± 1.22 17.2–20.6 8	18.86 ± 0.78 18.0–20.1 8	16.42 ± 0.95 15.3–18.1 8
M. crassipes San Josecito Cave	107.8* 1	26.7 1	10.2 1	10.1 1	9.1 1	23.10* 23.0–23.2* 2	19.1 1	18.5 1	14.9 1

[a] From Brodkorb 1964b; [b] larger measurement from Marsh 1872, and Shufeldt 1915.

* Slightly damaged specimen.

Table 17. Measurements (in mm) of the femur of female turkeys, with mean, standard deviation, observed range, and sample size. See Fig. 5 for explanation of measurements.

	Total Length	Proximal Width	Depth of Head	Width of Midshaft	Depth of Midshaft	Distal Width	Depth of Internal Condyle	Depth of External Condyle	Depth of Fibular Condyle
Meleagris cf. *M. leopoldi* or *M. anza*, Inglis IA	102.47* 99.4*–105.2* 3	23.35 23.0–23.7 2	8.88 8.6–9.2 4	9.73 9.1–10.2 6	8.45 8.2–8.9 6	21.70 21.3–22.0 3	17.72* 17.2*–18.7* 4	17.50 17.0–18.3 4	15.04 14.4–16.1 5
Meleagridinae, gen. and sp. indet. Gilliland[a,b]	—	25.5* 1	9.2* 1	—	—	—	—	—	—
Meleagris sp. Coleman IIA	—	27.4 1	9.6 1	11.2 1	10.6 1	23.7 1	21.2* 1	20.10 19.7–20.5 2	16.9* 1
Meleagris sp. Papago Springs Cave[b]	~110 1	~26.2 1	—	—	—	—	—	—	—
Meleagris cf. *M. gallopavo* Burnet Cave	—	—	—	10.7 1	9.6 1	—	—	—	—
Meleagris sp. Haile VIIA	114.4 1	26.3 1	9.9 1	10.3 1	9.6 1	24.0 1	20.2 1	19.7 1	17.0 1
Meleagris cf. *M. gallopavo* Reddick IB	—	—	—	—	—	23.5 1	—	19.1 1	16.8 1
M. gallopavo, Ichetucknee River	—	—	—	10.65 10.3–11.0 2	9.30 8.9–9.7 2	22.5* 1	18.6* 1	18.0* 1	16.0* 1
M. gallopavo Seminole Field	—	26.1 1	9.2 1	—	—	22.65 22.3–23.0 2	—	18.25 17.8–18.7 2	15.70 15.2–16.2 2
Meleagris sp. Hog Creek	—	26.8 1	9.8 1	—	—	—	—	—	—
Meleagris cf. *M. gallopavo* Sante Fe IA	115.4* 1	25.8* 1	—	11.8 1	9.9 1	23.3* 1	—	18.9* 1	17.4* 1
M. gallopavo Nichol's Hammock	104.10* 101.4–106.8* 2	24.70 24.0–25.4 2	8.80 8.6–9.0 2	9.75 9.5–10.0 2	8.65 8.2–9.1 2	21.00 20.2–21.8 2	—	17.65 17.5–17.8 2	15.45 15.3–15.6 2
M. gallopavo Good's Shellpit	—	—	8.5 1	10.2 1	9.1 1	—	—	—	—
M. gallopavo Buffalo Site	117.27 ± 3.17 112.9–122.0 9	27.42 ± 0.57 26.1–28.4 20	10.14 ± 0.41 9.5–11.0 24	11.22 ± 0.50 10.3–11.8 29	9.63 ± 0.42 8.9–10.3 29	23.85 ± 0.61 22.9–25.0 10	20.00 19.2–20.8 5	19.46 ± 0.44 18.4–20.0 14	17.02 ± 0.57 16.3–18.3 12
M. gallopavo silvestris, New York, Pennsylvania, Virginia	113.57 ± 3.16 108.9–119.0 12	26.28 ± 0.64 25.1–27.3 12	9.81 ± 0.31 9.3–10.2 12	10.68 ± 0.43 9.9–11.2 12	9.31 ± 0.52 8.6–10.1 12	22.87 ± 0.50 22.1–23.5 12	19.04 ± 0.54 17.9–19.9 12	18.52 ± 0.51 18.0–19.3 12	15.95 ± 0.51 15.1–16.7 12

Table 17. Continued.

	Total Length	Proximal Width	Depth of Head	Width of Midshaft	Depth of Midshaft	Distal Width	Depth of Internal Condyle	Depth of External Condyle	Depth of Fibular Condyle
M. gallopavo osceola, Florida	108.50 ± 2.49 104.0–113.9 11	25.33 ± 0.97 23.9–27.2 11	8.81 ± 0.34 8.2–9.2 11	10.46 ± 0.41 9.8–11.2 11	8.72 ± 0.48 8.1–9.7 11	21.16 ± 0.89 20.0–23.5 11	18.65 ± 0.83 17.8–20.5 11	17.78 ± 0.62 16.9–19.1 11	15.55 ± 0.79 14.8–17.3 11
M. gallopavo mexicana, Chihuahua, Coahuila, México	116.90 112.0–124.2 3	26.80 25.4–28.5 3	10.03 9.7–10.5 3	11.30 10.9–11.6 3	9.83 9.3–10.2 3	23.67 22.5–25.0 3	19.57 18.1–21.4 3	19.20 17.4–20.6 3	16.93 15.1–18.6 3
M. gallopavo merriami Arizona	115.80 112.4–119.3 3	27.17 26.9–27.5 3	10.03 9.8–10.4 3	11.20 11.0–11.4 3	9.97 9.9–10.1 3	23.67 23.3–23.9 3	18.73 18.1–19.1 3	18.47 18.0–18.8 3	16.23 15.9–16.8 3
M. gallopavo Total skeletal specimens[c]	112.01 ± 4.54 104.0–124.2 30	26.04 ± 1.04 23.9–28.5 30	9.43 ± 0.65 8.2–10.5 30	10.69 ± 0.49 9.8–11.6 30	9.18 ± 0.65 8.1–10.2 30	22.36 ± 1.23 20.0–25.0 30	18.92 ± 0.80 17.8–21.4 30	18.26 ± 0.83 16.9–20.6 30	15.90 ± 0.86 14.8–18.6 30
M. californica Rancho La Brea	104.66* ± 2.92 99.4–111.8* 23	25.35 ± 0.96 22.9–27.3 33	9.28 ± 0.42 8.3–10.1 33	10.03 ± 0.48 9.1–10.8 23	8.47 ± 0.42 7.7–9.2 23	22.03 ± 0.89 20.4–23.4 14	17.45 16.8–18.4 4	17.06 ± 0.70 15.7–17.8 17	15.28 ± 0.79 13.8–16.0 16
M. californica Carpinteria	103.90* 103.1–104.7* 2	25.60 24.3–27.1 6	9.40 8.7–9.8 6	10.32 9.9–10.8 4	8.52 8.3–8.9 4	22.20 21.8–22.4 4	17.8 1	17.58 17.2–18.1 4	15.38 15.1–16.0 4
M. californica Total specimens	104.60* ± 2.82 99.4*–111.8* 25	25.39 ± 0.97 22.9–27.3 39	9.29 ± 0.42 8.3–10.1 39	10.07 ± 0.48 9.1–10.8 27	8.48 ± 0.40 7.7–9.2 27	22.07 ± 0.79 20.4–23.4 18	17.52 16.8–18.4 5	17.16 ± 0.68 15.7–18.1 21	15.30 ± 0.72 13.8–16.0 20
M. ocellata Dzibilchaltún	98.0* 1	—	—	9.3 1	9.4 1	—	—	—	—
M. ocellata Yucatán, México, and Petén, Guatemala	97.54 ± 1.84 94.9–101.1 11	22.26 ± 0.81 20.9–23.7 11	8.11 ± 0.43 7.6–8.9 9	9.30 ± 0.46 8.7–10.1 11	8.37 ± 0.51 7.4–9.3 11	20.07 ± 0.47 19.3–21.0 11	16.33 ± 0.79 15.5–17.8 9	16.34 ± 0.46 15.6–17.0 9	14.26 ± 0.51 13.8–15.3 9
M. crassipes San Josecito Cave	94.05* 91.3*–96.8* 2	23.05 22.5–23.6 2	8.70 8.5–8.8 4	9.39 ± 0.55 8.6–10.3 8	8.51 ± 0.34 8.1–8.9 8	20.9* 1	—	16.0* 1	13.6 1

[a] From Brodkorb 1964b; [b] may possibly represent a male; [c] includes one specimen from northern Florida not identified to subspecies.

* Slightly damaged specimen.

Table 18. Measurements (in mm) of the tibiotarsus of male turkeys, with mean, standard deivation, observed range, and sample size. See Fig. 6 for explanation of measurements.

	Length Without Cnemial Crest†	Width of Head	Width of Midshaft	Depth of Midshaft	Distal Width	Depth of Internal Condyle	Depth of External Condyle
Meleagridinae cf. *Meleagris* Buckhorn	—	—	—	—	18.9* 1	19.1* 1	—
Meleagris sp. Haile XVA	—	—	~12.4 1	~9.9 1	18.4* 1	19.5* 1	17.9* 1
Meleagris cf. *M. leopoldi* or *M. anza*, Inglis IA	205.2 199.5–208.5 4	23.43 ± 0.72 22.5–24.8 10	11.74 ± 0.47 10.3–12.4 24	9.10 ± 0.40 8.3–9.8 25	19.58 ± 0.83 18.3–21.7 22	19.24* ± 0.58 18.6–20.5* 11	17.92* ± 0.75 16.8–19.8* 20
Meleagris sp. Haile XVIA	—	—	—	—	—	18.5* 1	—
Meleagris sp. Coleman IIA	208.5 207.0–210.0 4	25.10 ± 0.76 24.2–26.1 8	12.34 ± 0.52 11.5–13.0 9	9.34 ± 0.44 8.7–9.8 8	21.09 ± 0.47 20.3–21.6 10	21.08 20.6–21.8 6	18.95 ± 0.25 18.6–19.5 12
M. gallopavo Ingleside	—	—	12.1 1	9.1 1	21.50* 21.2*–21.8 2	20.30* 19.9*–20.7* 2	18.85* 18.7*–19.0 2
Meleagris cf. *M. gallopavo*, Frankstown Cave	—	—	—	—	21.90 21.9 2	21.05* 20.9*–21.2* 2	19.35* 19.2–19.5* 2
M. gallopavo Manalapan[a]	245 1	30[b] 1	12.5 1	10.5 1	17[c] 1	—	17.3 1
M. gallopavo Manalapan	243.75* 243[d]–244.5*[e] 2	—	—	—	18[c,d] 1	—	—
M. gallopavo Manalapan[f]	235.5* 233*–238* 2	26.3 1	11.75* 11.4*–12.1 2	9.95 9.8–10.1 2	20.0* 1	19.4* 1	17.9* 1
Meleagris cf. *M. gallopavo* Sante Fe IIA	213.0 1	24.2 1	12.6 1	9.1 1	20.9 1	19.8* 1	18.7* 1
Meleagris cf. *M. gallopavo* Rock Spring	—	—	11.8 1	9.0 1	—	—	—
Meleagris cf. *M. gallopavo* Reddick IB	233.5 1	25.30 24.1–26.5 2	13.0 1	10.3 1	21.9 1	22.4 1	20.2 1
M. gallopavo Aucilla River	—	—	—	—	21.0* 1	20.8* 1	19.0* 1
M. gallopavo Ichetucknee River	230.5 226.5–233.5 4	26.33 25.7–27.0 3	12.54 ± 1.10 10.7–14.1 11	9.85 ± 0.87 8.8–11.4 11	21.81* ± 1.06 20.4*–23.6* 12	21.18* ± 1.04 19.8–22.3* 9	19.92 ± 0.86 18.5–21.2 11
M. gallopavo Seminole Field	—	—	—	—	21.43 21.0–22.1 3	—	19.10 19.0–19.2 2
Meleagris sp. Oakhurst Quarry	—	—	—	—	21.0* 1	—	19.9* 1
Meleagris cf. *M. gallopavo* Sante Fe IA	—	—	—	—	19.3** 1	19.8** 1	17.5** 1
Meleagris sp. Sante Fe IVA	—	—	~12.2 1	~9.2 1	19.7* 1	—	—
Meleagris sp. Wekiva Run III	—	—	—	—	20.6* 1	20.9* 1	18.1* 1
M. gallopavo Nichol's Hammock	—	—	—	—	20.8 1	—	19.7 1
M. gallopavo Good's Shellpit	—	23.2 1	—	—	—	—	—

Table 18. Continued.

	Length Without Cnemial Crest†	Width of Head	Width of Midshaft	Depth of Midshaft	Distal Width	Depth of Internal Condyle	Depth of External Condyle
M. gallopavo Buffalo Site	230.0 226.0–234.0 2	26.25 25.5–27.0 2	12.33 ± 0.63 10.7–13.2 15	9.98 ± 0.52 9.0–11.1 15	22.50 ± 0.91 20.2–24.8 22	22.07 21.4–23.1 6	19.80 ± 0.64 18.1–21.3 34
M. gallopavo silvestris, New York, Pennsylvania, Virginia	220.3 ± 6.9 200.0–233.0 26	25.10 ± 0.59 24.0–26.2 23	12.15 ± 0.63 10.9–13.1 26	9.63 ± 0.46 8.8–10.4 26	21.93 ± 0.85 20.3–23.3 26	21.63 ± 0.82 20.1–22.9 25	19.53 ± 0.40 18.8–20.1 25
M. gallopavo osceola, Florida	231.9 ± 10.6 221.5–253.0 9	23.20 ± 0.92 21.6–24.5 9	11.79 ± 0.69 10.9–13.0 9	9.28 ± 0.40 8.8–10.1 9	20.70 ± 0.88 19.0–22.2 10	20.58 ± 1.29 18.1–22.6 10	18.79 ± 1.18 17.0–20.2 10
M. gallopavo intermedia, Texas	231.0 1	—	12.2 1	10.0 1	21.5 1	20.7 1	18.8 1
M. gallopavo, mexicana Chihuahua, México	227.0 1	26.2 1	12.8 1	10.3 1	23.5 1	23.1 1	20.4 1
M. gallopavo merriami, Arizona	225.5 1	24.8 1	12.5 1	10.0 1	22.6 1	22.7 1	19.6 1
M. gallopavo Total skeletal specimens	223.6 ± 9.1 200.0–253.0 38	24.62 ± 1.11 21.6–26.2 35	12.09 ± 0.64 10.9–13.1 38	9.59 ± 0.47 8.8–10.4 38	21.66 ± 1.03 19.0–23.5 39	21.38 ± 1.10 18.1–23.1 38	19.29 ± 0.74 17.0–20.4 38
M. californica Rancho La Brea	203.5 ± 6.2 192.0–212.0 15	23.27 ± 0.61 22.6–24.5 9	11.26 ± 0.53 10.9–11.9 18	8.96 ± 0.36 8.0–9.4 18	20.00 ± 0.54 19.3–20.9 23	19.79 ± 0.74 18.8–21.2 14	18.03 ± 0.72 17.2–19.9 21
M. californica Carpinteria	202.4 199.0–204.5 4	23.56 22.8–24.3 5	11.22 11.0–11.3 5	9.14 8.6–9.5 5	19.70 ± 0.36 19.2–20.3 11	19.76 ± 0.52 19.3–20.7 8	17.98 ± 0.30 17.6–18.6 9
M. californica Total specimens	203.2 ± 5.6 192.0–212.0 19	23.37 ± 0.60 22.6–24.5 14	11.25 ± 0.47 10.9–11.9 23	9.00 ± 0.36 8.0–9.5 23	19.90 ± 0.50 19.2–20.9 34	19.78 ± 0.65 18.8–21.2 22	18.02 ± 0.62 17.2–19.9 30
M. ocellata Dzibilchaltún	176.5 1	—	10.15 9.6–10.7 2	8.35 8.1–8.6 2	18.35 17.6–19.1 2	—	16.40 15.8–17.0 2
Meleagris cf. *M. ocellata* Macanché	—	—	—	—	19.0* 1	—	16.2** 1
M. ocellata Yucatán, México and Petén, Guatemala	183.50 ± 5.46 175.0–193.0 9	19.86 ± 1.11 18.4–21.8 10	10.08 ± 0.69 8.9–10.9 9	7.92 ± 0.49 7.3–8.6 9	17.86 ± 0.98 16.6–19.2 9	17.87 16.9–19.0 7	16.30 15.3–17.6 7
M. crassipes San Josecito Cave	164.0 163.5–164.5 2	20.0 1	10.4 1	8.0 1	18.1 1	17.1* 1	15.45* 15.2–15.7* 2

[a] From Cope, 1871; [b] abnormally large probably because of a difference in position of specimen during measurement; [c] abnormally small, probably because of misinterpretation of described measurement or fragmentary nature of specimen; [d] from Marsh 1872; [e] from Shufeldt 1915. This is probably the specimen which Marsh measured; [f] specimens measured by the author.

† Measurements accurate only to within 0.5 mm.

* Slightly damaged specimen.

** Moderately damaged specimen.

Table 19. Measurements (in mm) of the tibiotarsus of female turkeys, with mean, standard deviation, observed range, and sample size. See Fig. 6 for explanation of measurements.

	Length Without Cnemial Crest†	Width of Head	Width of Midshaft	Depth of Midshaft	Distal Width	Depth of Internal Condyle	Depth of External Condyle
Meleagridinae cf. *Meleagris* Westmoreland, Park[a,b]	—	18.5* 1	—	—	15.0* 1	16.1 1	14.0* 1
Meleagridinae cf. *Meleagris*, Bone Valley (Palmetto Mine)	—	—	—	—	16.8* 1	16.5* 1	14.9 1
Meleagris progenes Rexroad	—	—	—	—	14.5* 1	15.2* 1	13.0* 1
Meleagris cf. *M.* *leopoldi* or *M. anza* Inglis IA	—	18.72 18.4–19.4 4	9.85 9.5–10.2 2	7.80 7.7–7.9 2	16.07 16.0–16.1 3	15.85* 15.7*–16.1* 4	14.38* 13.9*–15.0 4
Meleagris sp. Coleman IIA	—	—	10.45 10.2–10.7 2	8.40 8.0–8.8 2	17.88 17.0–18.8 5	17.80* 17.2–18.7* 4	16.05 15.6–16.5 2
Meleagris cf. *M.* *gallopavo* Burnet Cave	—	—	10.3 1	8.3 1	18.4* 1	18.0* 1	16.3* 1
M. gallopavo Ingleside	—	—	—	—	17.9* 1	—	15.9 1
M. gallopavo Manalapan[c]	183 1	19 1	9.6 1	—	16.5 1	—	16 1
M. gallopavo Manalapan[d]	180* 1	—	—	—	17.0 1	17.4* 1	15.9 1
M. gallopavo Aucilla River	—	—	—	—	15.2* 1	17.0* 1	—
M. gallopavo Ichetucknee River	178.0 175.5–180.5 2	21.4 1	10.17 9.5–11.0 6	8.27 7.7–8.8 6	17.42* ± 1.11 15.2*–18.8 12	17.00* ± 1.03 14.8*–18.2 11	15.39* ± 0.89 13.7*–16.5 12
Meleagris sp. Kendrick	—	—	—	—	17.0 1	18.0* 1	15.8 1
M. gallopavo Seminole Field	—	—	—	—	17.0 1	16.2 1	15.30 14.7–16.0 3
Meleagris sp. Econfina River	176.0* 1	—	—	—	14.9* 1	—	14.9* 1
Meleagris sp. Hog Creek	—	—	—	—	18.3* 1	—	—
Meleagris sp. Santa Fe IVA	—	—	9.7 1	7.8 1	—	—	—
M. gallopavo Nichol's Hammock	172.3 169.5–174.0 3	17.30 17.1–17.7 3	8.54 8.2–9.0 5	7.04 6.9–7.1 5	15.67 15.1–16.8 3	15.93 15.8–16.1 3	14.55 14.1–15.0 4
M. gallopavo Good's Shellpit	—	—	—	—	16.6* 1	16.1* 1	14.5 1
M. gallopavo Buffalo Site	185.7 182.0–189.0 3	20.92 20.0–22.0 6	10.17 ± 0.42 9.5–10.9 16	8.17 ± 0.22 7.9–8.6 15	18.03 ± 0.55 16.9–19.0 28	18.29 ± 0.84 17.0–20.1 11	15.97 ± 0.56 15.0–17.0 32
M. gallopavo Hartman's Cave	—	—	—	—	18.00 17.9–18.1 2	16.45 16.1–16.8 2	15.45 15.1–15.8 2
M. gallopavo silvestris, New York, Pennsylvania, Virginia	175.7 ± 6.3 164.0–187.0 12	19.48 ± 0.45 18.9–20.2 9	9.24 ± 0.41 8.8–10.0 12	7.42 ± 0.33 7.0–8.0 12	17.42 ± 0.40 16.9–18.1 12	17.23 ± 0.39 16.5–17.9 12	15.58 ± 0.43 15.1–16.4 12
M. gallopavo osceola, Florida	178.1 ± 4.4 171.0–186.5 10	18.04 ± 0.65 17.3–19.6 11	9.17 ± 0.24 8.9–9.7 11	7.35 ± 0.30 6.8–7.8 11	16.44 ± 0.56 15.7–17.6 10	16.40 ± 0.62 15.4–17.5 10	14.92 ± 0.31 14.4–15.5 10
M. gallopavo mexicana, Chihuahua, Coahuila, México	183.5 178.0–190.0 3	20.07 19.5–21.2 3	10.17 9.8–10.5 3	7.90 7.6–8.1 3	18.40 17.2–19.3 3	18.17 17.0–19.6 3	16.13 14.8–17.3 3

Table 19. Continued.

	Length Without Cnemial Crest†	Width of Head	Width of Midshaft	Depth of Midshaft	Distal Width	Depth of Internal Condyle	Depth of External Condyle
M. gallopavo merriami, Arizona	175.5 170.0–181.0 2	19.73 19.1–20.3 3	9.83 9.5–10.1 3	8.13 7.5–8.9 3	17.60 17.6 2	17.55 17.2–17.9 2	15.30 15.3 2
M. gallopavo Total skeletal specimens[e]	177.0 ± 6.1 164.0–190.0 28	18.94 ± 1.01 17.3–21.2 27	9.35 ± 0.47 8.8–10.5 30	7.51 ± 0.43 6.8–8.9 30	17.12 ± 0.86 15.7–19.3 28	17.00 ± 0.86 15.4–19.6 28	15.43 ± 0.66 14.2–17.3 28
M. californica Rancho La Brea	168.4 ± 3.1 164.0–173.0 8	19.25 ± 0.54 18.4–19.9 8	9.25 ± 0.30 8.8–9.8 16	7.69 ± 0.37 6.9–8.3 16	16.74 ± 0.43 15.8–17.7 26	16.60 ± 0.38 15.6–17.3 25	15.11 ± 0.40 14.1–15.9 27
M. californica Carpinteria	168.7 165.0–174.0 3	18.8 1	9.70 9.5–10.0 3	7.50 7.4–7.7 3	16.66 16.1–17.3 5	16.66 15.6–17.8 5	15.00 14.3–15.5 6
M. californica Total specimens	168.4 ± 3.4 164.0–174.0 11	19.20 ± 0.53 18.4–19.9 9	9.32 ± 0.33 8.8–10.0 19	7.66 ± 0.35 6.9–8.3 19	16.73 ± 0.43 15.8–17.7 31	16.61 ± 0.46 15.6–17.8 30	15.09 ± 0.40 14.1–15.9 33
Meleagridinae cf. *Meleagris,* Workman and Alhambra Streets	—	—	—	—	16.3 1	—	14.5 1
M. ocellata Dzibilchaltún	—	—	7.9 1	7.0 1	15.4 1	14.6 1	13.2 1
M. ocellata Yucatán, México, and Petén, Guatemala	158.2 ± 4.7 150.5–167.0 9	17.14 ± 0.52 16.5–18.1 11	8.81 ± 0.23 8.5–9.1 9	7.11 ± 0.41 6.4–7.6 9	15.02 ± 0.46 14.2–16.0 10	14.95 ± 0.72 14.1–16.1 8	13.66 ± 0.50 13.1–14.5 8
M. crassipes San Josecito Cave	150.7* 150.0–152.0* 3	18.6 1	9.45 9.0–9.9 2	7.60 7.2–8.0 2	17.45 17.4–17.5 2	15.90* 15.8*–16.0* 2	14.18 13.7–14.6 4

[a] Based on two specimens which may represent opposite ends of the same bone; [b] may represent a male; [c] from Marsh 1872; [d] measured by the author—possibly the same as the specimen measured by Marsh; [e] includes one specimen from northern Florida not identified to subspecies.

† Measurements accurate only to within 0.5 mm.

* Slightly damaged specimen.

Table 20. Measurements (in mm) of the tarsometatarsus of male turkeys, with mean, standard deviation, observed range and sample size. See Fig. 7 for explanation of measurements.

	Total Length A	Proximal Width B	Least Width of Shaft C	Least Depth of Shaft D	Proximal End to Middle of Spur Core E	Top of Spur Core to End of Middle Trochlea F
Proagriocharis kimballensis UNSM Coll. Loc. Ft-40	98[c] 1	14[c] 1	—	—	58 1	—
Meleagris progenes, Rexroad	—	—	—	4.9 1	—	53.6 1
Meleagris cf. *M. progenes,* Benson	113.5 1	18.7 1	7.45 7.1–7.8 2	5.05 5.0–5.1 2	64.9 1	51.90 50.0–53.8 2
M. leopoldi Cita Canyon	139.5 1	21.0 1	8.7 1	6.0 1	88.8 1	~56.9 1
Meleagris cf. *M. leopoldi* or *M. anza,* Inglis IA	151.88 ± 3.88 146.6–158.0 8	22.06 ± 0.59 21.1–23.7 26	9.24 ± 0.44 8.4–9.9 26	5.95 ± 0.25 5.3–6.5 30	96.14 ± 2.92 91.6–101.1 14	59.82 ± 2.99 52.8–63.8 13
Meleagris sp. Coleman IIA	153.06 149.4–157.0 5	23.98 ± 0.30 23.6–24.5 8	9.60 ± 0.48 9.1–10.5 11	6.32 ± 0.21 6.0–6.7 13	90.87 86.5–96.3 6	67.04 59.7–70.4 7
M. gallopavo American Falls	165.5* 1	—	9.8 1	6.2 1	95.5* 1	74.4 1
M. gallopavo Ingleside	161.5 1	24.3* 1	9.4 1	6.2 1	94.50 93.0–96.0 2	72.5 1
M. gallopavo Manalapan	176.5[e] 1	23.35 23[e]–23.7[f] 2	—	—	110[e] 1	—
Meleagris cf. *M. gallopavo,* Santa Fe River IIA	—	—	8.9 1	6.1 1	98.3 1	67.8 1
Meleagris sp. Bradenton	—	23.8 1	—	—	—	—
Meleagris sp. Withlacoochee River	—	—	7.8 1	5.1 1	—	~65.8 1
Meleagris cf. *M. gallopavo* Reddick IB	166.25* 161.5–171.0* 2	24.8 1	9.20 9.0–9.4 2	6.23 6.2–6.3 3	97.75* 97.2*–98.3 2	73.55 68.8–78.3 2
Meleagris cf. *M. gallopavo* Melbourne	—	23.9 1	—	—	—	—
Meleagris cf. *M. gallopavo* Sabertooth Cave	—	—	—	—	—	—
M. gallopavo Aucilla River	—	—	8.2 1	6.8 1	—	77.2 1
M. gallopavo Ichetucknee River	173.75 170.0–177.5 2	23.99 ± 0.89 22.3–25.3 8	8.90 ± 0.83 7.5–10.1 11	5.87 ± 0.40 5.2–6.7 19	103.23 101.0–106.7 3	73.16 ± 2.88 68.7–77.1 8
Meleagris sp. Kendrick IA	—	22.2 1	—	—	—	—
M. gallopavo Seminole Field	—	23.9* 1	9.0 1	5.75 5.7–5.8 2	—	—
Meleagris cf. *M. gallopavo* Bowman IA	—	—	8.6 1	—	—	—
Meleagris cf. *M. gallopavo,* Santa Fe River IA	—	—	8.1 1	5.2 1	—	—
M. gallopavo Wacissa River	—	24.1* 1	9.2 1	—	103.1 1	—

Table 20. Continued.

Middle of Spur Core to End of Middle Trochlea G	Width of Spur Core H[a]	Length of Spur Core J[b]	Angle of Spur Core (in Degrees) K	Distal Width L	Depth of Inner Trochlea M	Depth of Middle Trochlea N	Depth of Outer Trochlea P
40[c] 1	6.2 1	15.7* 1	38[c] 1	—	—	—	—
48.0 1	7.1 1	—	49 1	19.0 1	8.4 1	9.1 1	9.9* 1
48.95 48.6–49.3 2	—	—	56 1	18.9 1	8.7 1	9.45 9.0–9.9 2	10.0 1
50.7 1	—	—	55.75[d] 53.0–58.5 2	21.0 1	9.5 1	10.2 1	11.2 1
55.13 ± 3.12 48.3–59.6 13	7.70 ± 0.86 6.1–10.3 37	31.21* ± 2.78 26.2*–35.5* 15	47.4 ± 3.4 43–56 28	21.68 ± 0.52 20.9–22.7 15	9.56 ± 0.38 8.9–9.9 11	10.58 ± 0.37 10.0–11.1 20	10.88 ± 0.52 10.1–11.8 8
61.86 54.9–65.1 7	7.53 ± 0.50 7.0–8.2 9	28.82* 21.1*–32.4* 4	52.9 ± 4.0 45–58 10	23.75 ± 1.08 22.0–24.8 8	10.68 10.0–11.5 5	12.04 ± 0.30 11.7–12.5 8	12.98 12.0–13.9 5
70.0 1	7.0 1	17.4 1	50 1	26.0 1	—	12.1 1	13.1 1
68.5 1	6.70 6.5–6.9 2	—	55.0 55 2	23.5 1	10.0 1	10.8 1	12.0 1
66.5[e] 1	—	—	—	—	—	—	—
62.9 1	5.8 1	—	58 1	—	—	10.6 1	—
—	—	—	—	—	—	—	—
~60.3 1	—	—	—	—	—	—	—
68.20 63.2–73.2 2	—	—	65 1	24.03 23.8–24.3 3	10.83 10.4–11.1 3	11.77 11.1–12.1	12.75 12.5–13.0 2
—	6.5 1	—	—	—	—	—	—
—	6.4 1	19.0* 1	—	—	—	—	—
68.2 1	6.1 1	20.0* 1	63 1	24.8 1	—	11.9 1	13.7* 1
68.55 ± 2.94 63.9–72.5 8	6.70 5.9–7.6 5	19.53* 16.1*–21.7* 3	57.1 ± 5.0 46–66 12	23.44 ± 1.50 21.1–26.2 9	10.13 9.3–11.0 6	11.38 ± 0.69 10.2–12.4 12	12.85 12.3–13.5 4
—	—	—	—	—	—	—	—
—	6.32 ± 0.68 5.1–7.5 12	16.60* 15.0*–17.9* 3	—	—	10.30 10.0–10.6 2	11.30 11.0–11.6 2	—
—	5.9 1	—	58 1	—	—	—	—
68.0 1	—	—	—	22.0 1	—	10.3* 1	—
—	6.1 1	17.3* 1	67 1	—	—	—	—

Continued

Table 20. Continued.

	Total Length A	Proximal Width B	Least Width of Shaft C	Least Depth of Shaft D	Proximal End to Middle of Spur Core E	Top of Spur Core to End of Middle Trochlea F
M. gallopavo Buffalo Site	168.0 1	24.72 ± 0.91 22.9–26.8 22	9.13 ± 0.47 8.0–9.9 27	6.25 ± 0.26 5.7–6.8 27	98.8 1	76.0 1
M. gallopavo Hartman's Cave	—	—	—	—	—	—
M. gallopavo silvestris, New York, Pennsylvania, Virginia	160.55 ± 5.92 146.0–172.5 31	24.49 ± 1.13 22.3–27.3 32	9.34 ± 0.58 8.0–10.8 33	6.04 ± 0.39 5.2–6.9 32	91.48 ± 4.44 81.3–101.3 25	73.14 ± 3.59 65.4–78.0 25
M. gallopavo osceola, Florida	176.55 ± 8.51 166.5–192.5 10	23.11 ± 0.99 21.7–24.9 10	8.96 ± 0.68 8.1–9.9 10	5.94 ± 0.44 5.5–7.0 10	105.96 98.2–117.2 7	72.92 70.6–74.0 5
M. gallopavo intermedia, Texas	172.0 1	23.8 1	9.1 1	6.1 1	103.2 1	72.7 1
M. gallopavo mexicana, Chihuahua, Méx.	160.5 1	26.2 1	9.6 1	6.6 1	92.6 1	71.8 1
M. gallopavo Total skeletal specimens	164.53 ± 9.40 146.0–192.5 43	24.20 ± 1.25 21.7–27.3 44	9.26 ± 0.61 8.0–10.8 45	6.03 ± 0.40 5.2–7.0 44	94.84 ± 7.70 81.3–117.2 34	73.05 ± 3.22 65.4–78.0 32
M. californica Rancho La Brea	140.16 ± 4.79 130.6–149.5 50	22.05 ± 0.84 20.5–24.0 34	8.81 ± 0.34 8.1–9.7 45	5.81 ± 0.26 5.3–6.3 49	79.41 ± 3.81 69.7–86.9 49	64.62 ± 2.89 58.7–70.4 48
M. californica Carpinteria	141.60 140.5–144.0 5	22.32 22.1–22.5 5	8.74 ± 0.21 8.5–9.1 8	5.79 ± 0.19 5.6–6.0 8	81.26 80.3–82.7 5	64.77 62.8–66.5 7
M. californica Total specimens	140.29 ± 4.60 130.6–149.5 55	22.08 ± 0.78 20.5–24.0 39	8.80 ± 0.32 8.1–9.7 53	5.80 ± 0.25 5.3–6.3 57	79.58 ± 3.68 69.7–86.9 54	64.64 ± 2.72 58.7–70.4 55
M. ocellata Dzibilchaltún	140.0 1	20.0 1	7.8 1	5.10 4.9–5.3 3	84.6 1	60.9 1
Meleagris cf. *M. ocellata* Cancún Island	—	—	—	4.6 1	—	—
M. ocellata Mayapán	136.38 ± 4.96 128.0–145.5 17	22.56 ± 0.53 21.9–23.6 12	8.42 ± 0.50 7.5–9.0 15	6.05 ± 0.35 5.3–6.8 17	84.1 1	65.2 1
M. ocellata Yucatán, México and Petén, Guatemala	138.12 ± 4.41 130.2–146.0 14	20.36 ± 0.88 19.1–21.9 14	7.77 ± 0.57 6.3–9.0 14	5.30 ± 0.37 4.6–5.8 12	85.08 ± 3.86 78.6–91.0 13	58.20 ± 2.47 53.2–61.7 13
M. crassipes San Josecito Cave (spurred specimens only)[g]	108.30* 103.7–114.4 3	—	7.83 7.5–8.3 3	4.70 4.5–4.9 3	59.83* 57.8*–61.3* 3	54.15* 49.9*–58.4 2
M. crassipes San Josecito Cave (all specimens)[h]	102.68 ± 5.18 96.1*–114.4 10	17.85 17.5–18.2 2	7.51 ± 0.42 6.6–8.3 16	4.60 ± 0.21 4.0–4.9 15	59.83* 57.8*–61.3* 3	54.15* 49.9*–58.4 2

Table 20. Continued.

Middle of Spur Core to End of Middle Trochlea G	Width of Spur Core H[a]	Length of Spur Core J[b]	Angle of Spur Core (in Degrees) K	Distal Width L	Depth of Inner Trochlea M	Depth of Middle Trochlea N	Depth of Outer Trochlea P
70.15 69.2–71.1 2	6.62 ± 0.49 5.8–7.9 18	21.97* 19.2*–25.8* 7	60.8 ± 4.4 56–69 13	24.57 ± 0.80 23.1–25.8 13	11.27 ± 0.55 10.2–11.9 9	12.18 ± 0.54 11.2–12.9 18	12.91 ± 0.33 12.2–13.3 8
—	—	—	—	23.6 1	—	12.0 1	—
68.90 ± 3.12 62.1–73.2 27	6.64 ± 0.84 5.4–8.7 21	20.84 ± 2.52 16.8–24.9 14	61.7 ± 5.1 54–73 26	24.53 ± 1.08 21.9–26.6 33	10.90 ± 0.69 9.5–12.4 32	12.01 ± 0.44 10.8–13.0 32	12.85 ± 0.60 11.5–14.0 32
70.04 65.8–74.8 7	6.32 6.1–6.5 4	22.48 22.2–23.0 4	63.4 57–68 5	22.46 ± 1.19 20.2–24.1 10	10.18 ± 0.36 9.7–10.9 10	11.11 ± 0.55 10.1–11.9 10	12.08 ± 0.85 11.3–14.1 10
68.8 1	7.5 1	22.5 1	55 1	23.4 1	—	—	—
67.9 1	6.4 1	—	56 1	27.8 1	12.2 1	12.3 1	13.1 1
69.09 ± 3.05 62.1–74.8 36	6.61 ± 0.76 5.4–8.7 27	21.27 ± 2.27 16.8–24.9 19	61.6 ± 5.2 54–73 33	24.12 ± 1.49 20.2–27.8 45	10.76 ± 0.73 9.5–12.4 43	11.81 ± 0.60 10.1–13.0 43	12.68 ± 0.73 11.3–14.1 43
60.77 ± 2.82 55.7–66.5 49	5.94 ± 0.58 4.9–7.6 47	18.60* ± 2.16 14.9*–22.8* 31	61.2 ± 4.9 54–70 47	22.53 ± 0.74 20.9–24.6 46	10.00 ± 0.48 9.0–11.1 37	10.88 ± 0.38 10.1–11.6 43	11.74 ± 0.56 10.4–12.7 35
60.60 58.3–62.4 7	6.11 5.5–6.9 7	18.87* 15.3*–21.8 7	61.3 56–67 6	22.63 21.3–23.3 7	10.00 9.8–10.5 6	11.20 10.8–11.4 7	12.03 11.6–12.4 6
60.75 ± 2.67 55.7–66.5 56	5.96 ± 0.58 4.9–7.6 54	18.65* ± 2.13 14.9*–22.8* 38	61.2 ± 4.9 54–70 53	22.54 ± 0.73 20.9–24.6 53	10.00 ± 0.45 9.0–11.1 43	10.93 ± 0.37 10.1–11.6 50	11.79 ± 0.54 10.4–12.7 41
55.4 1	6.70 6.2–7.2 2	—	45 1	21.0 1	—	9.8 1	—
—	—	—	—	—	—	—	—
61.4 1	—	—	55 1	21.63 ± 0.87 20.2–22.9 15	—	10.90 10.7–11.1 2	—
54.41 ± 2.65 50.2–57.4 13	6.16 ± 0.67 4.8–7.3 11	27.25 ± 2.68 24.1–32.2 11	50.2 ± 4.6 43–58 13	19.91 ± 1.17 18.0–21.8 14	9.47 ± 0.64 8.1–10.4 11	9.81 ± 0.43 9.0–10.8 12	10.83 ± 0.72 9.1–12.0 12
48.47* 45.5*–54.0 3	7.0 1	12.6* 1	36 1	19.8 1	9.9 1	9.40* 8.8*–10.0 2	11.0 1
48.47* 45.5*–54.0 3	7.0 1	12.6* 1	36 1	18.70 18.2–19.8 4	9.33 8.8–9.9 3	8.93 8.3–10.0 6	10.38 9.9–11.0 4

[a] Only relatively smooth adult spur cores considered; [b] only fully pointed spur cores considered; [c] from Martin and Tate 1970; [d] from A.H. Miller and Bowman 1956; [e] from Marsh 1872. Undoubtedly the same specimen as measured by Shufeldt 1915; [f] specimens measured by the author; [g] may include a specimen which represents a female; [h] probably includes specimens which represent females.

* Slightly damaged specimen.

Table 21. Measurements (in mm) of the tarsometatarsus of female turkeys, with mean, standard deviation, observed range, and sample size. See Fig. 7 for explanation of measurements.

	Total Length	Proximal Width	Least Width of Shaft	Least Depth of Shaft	Distal Width	Depth of Inner Trochlea	Depth of Middle Trochlea	Depth of Outer Trochlea
Rhegminornis calobates[a] Thomas Farm	—	8.1* 1	3.9 1	2.55 2.2–2.9 2	9.5 1	—	4.40* 4.2*–4.6 2	—
Proagriocharis kimballensis, UNSM Coll. Loc. Ft-40	~78 1	12.95 12.8–13.1 2	5.05 4.9–5.2 2	3.5 1	—	—	—	—
Meleagris progenes, Rexroad	—	—	—	3.9 1	—	—	8.1 1	—
Meleagris cf. *M. leopoldi* or *M. anza,* Inglis IA	124.83* 123.0*–126.0 3	17.38* 16.4*–18.1* 5	7.60 7.2–8.0 2	5.08 4.8–5.5 6	17.85 17.8–17.9 2	8.30 7.9–8.7 2	8.93 8.9–9.0 3	9.2 1
Meleagris sp. Coleman IIA	130.8 1	19.67 18.4–20.5 3	8.0 1	5.8 1	19.55 19.2–19.9 2	8.1 1	9.65 9.6–9.7 2	10.5 1
Meleagris cf. *M. gallopavo* Carlisle Cave	—	18.1 1	6.8 1	4.8 1	18.1 1	8.6 1	8.9 1	9.7 1
M. gallopavo Manalapan	—	19[b] 1	—	—	—	—	—	—
M. gallopavo Ichetucknee River	136.80 135.1–139.7 3	20.76 ± 0.68 20.0–22.1 8	7.94 7.7–8.8 5	5.30 4.9–5.9 7	19.62 18.0–21.1 5	8.64 8.2–8.9 5	10.12 9.6–10.7 5	10.82 10.3–11.7 5
M. gallopavo Seminole Field	—	18.94 18.1–20.2 5	7.17 7.1–7.3 3	4.80 4.6–4.9 5	18.9 1	8.77 8.5–9.0 3	9.25 9.1–9.4 2	—
Meleagris cf. *M. gallopavo* Haile IIA	—	—	7.8 1	5.0 1	—	—	9.9 1	10.6 1
M. gallopavo Nichol's Hammock	—	—	6.77 6.5–7.0 3	4.57 4.4–4.7 3	17.50 17.0–18.1 3	7.70 7.2–8.2 2	8.70 8.5–9.0 3	8.4 1
M. gallopavo Buffalo Site, West Virginia	136.25 133.0–140.0 4	19.91 ± 0.99 18.0–22.7 15	7.42 ± 0.44 6.5–8.1 21	5.00 ± 0.29 4.2–5.7 31	19.87 ± 0.88 18.2–21.2 15	8.92 ± 0.58 8.2–10.0 10	9.68 ± 0.55 9.1–10.5 17	10.88 ± 0.50 9.9–11.9 13
M. gallopavo Hartman's Cave	—	—	—	—	—	—	9.8 1	—
M. gallopavo silvestris, New York, Pennsylvania, Virginia	126.90 ± 5.08 115.2–134.0 19	19.46 ± 0.63 18.3–20.7 20	7.32 ± 0.45 6.6–8.2 20	4.94 ± 0.19 4.6–5.3 19	19.72 ± 0.78 18.2–21.0 20	8.70 ± 0.51 8.0–9.8 20	9.60 ± 0.30 9.1–10.1 20	10.15 ± 0.54 9.3–11.1 20
M. gallopavo osceola Florida	131.68 ± 4.00 125.0–137.0 11	18.30 ± 0.67 17.9–20.2 11	6.96 ± 0.32 6.3–7.3 11	4.84 ± 0.11 4.6–5.0 11	17.76 ± 0.98 15.8–19.0 11	8.02 ± 0.46 7.2–8.8 11	8.98 ± 0.46 8.2–9.7 11	9.64 ± 0.54 9.0–10.7 11
M. gallopavo mexicana Chihuahua, México	134.90 130.3–139.5 2	21.55 20.6–22.5 2	7.65 7.4–7.9 2	5.40 5.1–5.7 2	21.85 21.5–22.2 2	9.90 9.4–10.4 2	10.20 9.9–10.5 2	11.15 10.9–11.4 2
M. gallopavo Total skeletal specimens[c]	128.74 ± 5.58 115.2–139.5 33	19.14 ± 1.09 17.2–22.5 34	7.21 ± 0.44 6.3–8.2 34	4.92 ± 0.24 4.3–5.7 33	19.15 ± 1.42 15.8–22.2 34	8.51 ± 0.70 7.2–10.4 34	9.41 ± 0.50 8.2–10.5 34	10.02 ± 0.64 9.0–11.4 34
M. californica Rancho La Brea	114.85 ± 3.92 105.7–122.3 32	18.36 ± 0.64 17.5–19.8 25	7.05 ± 0.32 6.5–7.6 32	4.84 ± 0.22 4.5–5.3 32	18.75 ± 0.61 17.6–19.9 32	8.44 ± 0.40 7.9–9.4 23	9.28 ± 0.38 8.4–10.0 32	9.98 ± 0.45 9.2–10.9 24
M. californica Carpinteria	116.00 112.3–119.7 2	18.88 18.6–19.2 4	7.15 7.1–7.2 2	4.95 4.8–5.1 4	19.20 19.0–19.5 4	8.62 8.4–9.0 4	9.62 9.4–9.8 4	10.12 9.8–10.6 4

Table 21. Continued.

	Total Length	Proximal Width	Least Width of Shaft	Least Depth of Shaft	Distal Width	Depth of Inner Trochlea	Depth of Middle Trochlea	Depth of Outer Trochlea
M. californica Total specimens	114.92 ± 3.91 105.7–122.3 34	18.43 ± 0.63 17.5–19.8 29	7.05 ± 0.31 6.5–7.6 34	4.85 ± 0.21 4.5–5.3 36	18.80 ± 0.59 17.6–19.9 36	8.47 ± 0.38 7.9–9.4 27	9.32 ± 0.37 8.4–10.0 36	10.00 ± 0.44 9.2–10.9 28
Meleagris cf. *M. ocellata* Barton Ramie Site	—	17.4 1	—	—	—	—	—	—
M. ocellata Mayapán	121.50 120.5–122.5 2	20.60* 20.4*–20.8* 2	8.15 8.0–8.3 2	5.75 5.5–6.0 2	20.65 20.1–21.2 2	—	—	—
M. ocellata Yucatán, México and Petén, Guatemala	116.86 ± 4.14 111.9–124.5 11	16.98 ± 0.56 16.0–18.0 11	6.31 ± 0.35 5.8–7.0 11	4.56 ± 0.36 3.9–4.9 9	16.33 ± 0.97 14.5–17.8 11	7.97 ± 0.47 7.1–8.9 9	8.31 ± 0.35 7.9–9.0 9	9.32 ± 0.45 8.7–10.0 9
M. crassipes San Josecito Cave (unspurred specimens only)[d]	100.27* 96.1*–103.6 7	17.85 17.5–18.2 2	7.44 ± 0.41 6.6–8.2 13	4.58 ± 0.22 4.0–4.8 12	18.33 18.2–18.6 3	9.05 8.8–9.3 2	8.70 8.3–9.0 4	10.17 9.0–10.4 3

[a] May represent a male; [b] from Marsh 1872; [c] includes one specimen from northern Florida not identified to subspecies; [d] may include some specimens which represent males.

* Slightly damaged specimen.

Table 22. Ratios (in percent) of the measurements of the tarsometatarsus of male turkeys, with mean, standard deviation, observed range, and sample size. See Fig. 7 for explanation of measurements.

	B/A	B/E	C/A	D/A	D/C	F/A
Proagriocharis kimballensis, UNSM Coll. Loc. Ft-40	14.3[a] 1	24.1[a] 1	—	—	—	—
Meleagris cf. *M. progenes*, Benson	16.5 1	28.8 1	6.2 1	4.5 1	67.95 64.1–71.8 2	44.0 1
M. leopoldi Cita Canyon	15.0 1	23.6 1	6.2 1	4.3 1	69.0 1	~40.8 1
Meleagris cf. *M. leopoldi* or *M. anza*, Inglis IA	14.33 13.8–14.8 7	22.68 ± 0.85 21.1–23.6 12	6.00 ± 0.28 5.7–6.4 8	3.82 ± 0.28 3.2–4.1 8	64.40 ± 3.92 56.8–71.4 18	40.20 39.2–41.8 7
Meleagris sp. Coleman IIA	15.72 15.2–16.2 4	26.37 25.4–27.9 3	6.30 6.0–6.6 4	4.06 3.9–4.4 5	65.58 ± 2.12 61.9–68.5 9	44.10 39.5–46.6 3
M. gallopavo American Falls	—	—	5.9* 1	3.7* 1	63.3 1	45.0* 1
M. gallopavo Ingleside	14.1* 1	26.1* 1	5.8 1	3.8 1	66.0 1	44.9 1
M. gallopavo Manalapan[c]	13.0 1	20.9 1	—	—	—	—
Meleagris cf. *M. gallopavo*, Santa Fe River IIA	—	—	—	—	68.5 1	—
Meleagris sp. Withlacoochee River	—	—	—	—	65.4 1	—
Meleagris cf. *M. gallopavo* Reddick IB	15.4 1	25.2 1	5.55* 5.3*–5.8 2	3.75* 3.7*–3.8 2	68.00 66.0–70.0 2	44.20* 42.6–45.8* 2
Meleagris cf. *M. gallopavo* Sabertooth Cave	—	—	—	—	—	—
M. gallopavo Aucilla River	—	—	—	—	—	—
M. gallopavo Ichetucknee River	14.00 13.4–14.6 2	23.47 22.2–24.4 3	5.50 5.2–5.8 2	3.55 3.4–3.7 2	66.74 ± 4.68 63.0–77.3 9	42.25 42.1–42.4 2
M. gallopavo Seminole Field	—	—	—	—	—	—
Meleagris cf. *M. gallopavo*, Santa Fe River IA	—	—	—	—	64.2 1	—
M. gallopavo Wacissa River	—	23.4* 1	—	—	—	—
M. gallopavo Buffalo Site	14.8 1	25.2 1	5.4 1	3.8 1	69.11 ± 3.24 64.6–73.8 11	—
M. gallopavo silvestris, New York, Pennsylvania, Virginia	15.27 ± 0.72 13.8–16.7 31	27.11 ± 1.23 23.9–29.1 25	5.82 ± 0.41 5.0–6.6 31	3.76 ± 0.25 3.2–4.3 30	64.70 ± 3.06 58.8–74.7 32	45.59 ± 1.24 43.2–48.1 24
M. gallopavo osceola, Florida	13.10 ± 0.57 12.4–14.2 10	21.71 19.8–23.9 7	5.08 ± 0.38 4.5–5.7 10	3.40 ± 0.31 3.1–4.0 10	66.51 ± 5.55 59.1–77.8 10	41.78 39.6–43.5 5
M. gallopavo intermedia, Texas	13.8 1	23.1 1	5.3 1	3.5 1	67.0 1	42.3 1
M. gallopavo mexicana, Chihuahua, México	16.1 1	28.3 1	5.7 1	4.1 1	68.7 1	44.7 1
M. gallopavo Total skeletal specimens	14.75 ± 1.16 12.4–16.7 43	25.91 ± 2.59 19.8–29.1 34	5.64 ± 0.50 4.5–6.6 43	3.68 ± 0.31 3.1–4.3 42	65.25 ± 3.76 58.8–77.8 44	44.84 ± 1.94 39.6–48.1 31
M. californica Rancho La Brea	15.70 ± 0.62 14.5–17.1 34	27.85 ± 1.58 24.0–32.0 33	6.26 ± 0.21 5.9–6.7 45	4.13 ± 0.18 3.8–4.6 49	66.04 ± 2.84 60.2–74.1 45	46.11 ± 1.62 41.8–49.5 48

Table 22. Continued.

G/A	H/J	J/A	K/A	L/A	M/A	N/A	P/A
40.8[a] 1	39.5* 1	16.0*[a,b] 1	38.8[a] 1	—	—	—	—
42.8 1	—	—	—	16.6 1	7.7 1	7.9 1	8.8 1
36.3 1	—	—	—	15.0 1	6.8 1	7.3 1	8.0 1
36.74 35.6–38.5 7	25.68* ± 1.83 23.2–29.0 14	20.35* 18.5*–22.2* 6	31.98 28.9–35.1 6	14.26 13.7–14.8 7	6.24 5.9–6.7 5	6.86 ± 0.31 6.4–7.3 8	6.96 6.7–7.3 5
40.47 36.3–43.1 3	27.10* 22.0*–34.1* 4	17.85* 14.0*–21.7* 2	36.45* 33.7*–38.4 4	15.50 14.8–15.8 4	6.7 1	7.75 7.6–7.9 2	8.1 1
42.3* 1	40.2 1	10.5* 1	30.2* 1	15.7* 1	—	7.3* 1	7.9* 1
42.4 1	—	—	34.0 1	14.6 1	6.2 1	6.7 1	7.4 1
37.7 1	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—
40.95* 39.1–42.8* 2	—	—	38.0* 1	14.40* 13.9*–14.9 2	6.45* 6.4–6.5* 2	7.00* 6.9–7.1* 2	7.65* 7.3*–8.0 2
—	33.7* 1	—	—	—	—	—	—
—	30.5* 1	—	—	—	—	—	—
39.95 39.9–40.0 2	36.5* 1	9.1* 1	36.85 36.5–37.2 2	13.65 13.3–14.0 2	6.00 5.5–6.5 2	6.95 6.6–7.3 2	7.40 6.9–7.9 2
—	38.40* 36.1*–40.0* 3	—	—	—	—	—	—
—	—	—	—	—	—	—	—
—	35.3* 1	—	—	—	—	—	—
41.2 1	30.90* 27.0*–33.8* 7	—	33.3 1	—	7.0 1	7.4 1	—
42.92 ± 1.29 40.8–45.2 25	32.09 ± 3.08 28.7–40.0 13	12.82 ± 1.35 10.4–14.7 14	38.57 ± 3.54 33.3–45.3 25	15.32 ± 0.69 13.6–16.9 31	6.81 ± 0.37 6.2–7.5 30	7.51 ± 0.31 6.8–8.2 30	8.02 ± 0.40 6.8–8.8 30
39.81 37.3–43.2 7	28.15 27.5–28.4 4	13.05 13.0–13.2 4	36.28 32.8–40.0 5	12.72 ± 0.57 11.8–13.4 10	5.77 ± 0.25 5.2–6.1 10	6.28 ± 0.20 5.9–6.5 10	6.85 ± 0.51 6.4–8.1 10
40.0 1	33.3 1	13.1 1	32.0 1	13.6 1	—	—	—
42.3 1	—	—	34.9 1	17.3 1	7.6 1	7.7 1	8.2 1
42.18 ± 1.92 37.3–45.2 34	31.28 ± 3.12 27.5–40.0 18	12.88 ± 1.15 10.4–14.7 19	37.89 ± 3.67 32.0–45.3 32	14.72 ± 1.35 11.8–17.3 43	6.58 ± 0.58 5.2–7.6 41	7.22 ± 0.61 5.9–8.2 41	7.74 ± 0.66 6.4–8.8 41
43.35 ± 1.60 39.2–46.6 49	33.18* ± 3.76 27.6*–46.0* 31	13.18* ± 1.48 10.2*–15.3* 31	43.68 ± 3.59 37.4–52.1 47	16.11 ± 0.42 15.0–16.9 46	7.10 ± 0.30 6.4–7.7 37	7.76 ± 0.27 7.2–8.3 43	8.35 ± 0.37 7.5–9.0 35

Continued

Table 22. Continued.

	B/A	B/E	C/A	D/A	D/C	F/A
M. californica Carpinteria	15.78 15.5–16.0 4	27.58 27.3–27.8 4	6.25 6.0–6.5 4	4.16 4.0–4.3 5	66.31 63.6–69.8 7	45.62 44.5–46.2 5
M. californica Total specimens	15.71 ± 0.59 14.5–17.1 38	27.82 ± 1.49 24.0–32.0 37	6.26 ± 0.21 5.9–6.7 49	4.13 ± 0.17 3.8–4.6 54	66.08 ± 2.74 60.2–74.1 52	46.06 ± 1.56 41.8–49.5 53
M. ocellata Dzibilchaltún	14.3 1	23.6 1	5.6 1	3.8 1	67.9 1	43.5 1
M. ocellata Mayapán	16.71 ± 0.61 15.6–17.5 12	—	6.15 ± 0.33 5.5–6.6 15	4.44 ± 0.18 3.9–4.7 17	71.87 ± 2.76 68.2–76.2 15	44.8 1
M. ocellata Yucatán, México and Petén, Guatemala	14.74 ± 0.59 13.9–15.9 14	23.99 ± 1.28 22.3–26.6 13	5.61 ± 0.31 4.8–6.2 14	3.82 ± 0.18 3.5–4.1 12	68.30 ± 3.83 61.1–73.4 12	41.97 ± 1.99 38.2–45.2 13
M. crassipes San Josecito Cave (spurred specimens only)	—	—	7.20* 7.0*–7.4 3	4.33* 4.2*–4.5 3	60.00 59.0–61.0 3	49.55* 48.1*–51.0 2
M. crassipes San Josecito Cave (all specimens)	17.55 16.9–18.2 2	—	7.40* ± 0.33 7.0*–8.0* 10	4.55* ± 0.20 4.2*–4.9* 10	61.55 ± 3.15 54.8–66.7 15	49.55 48.1*–51.0 2

Table 22. Continued.

G/A	H/J	J/A	K/A	L/A	M/A	N/A	P/A
42.58	32.57*	13.12*	44.80	16.22	7.13	7.88	8.62
41.3–43.3	26.9*–35.9*	10.8*–15.4*	39.6–47.7	16.0–16.5	7.0–7.3	7.7–8.0	8.3–8.8
5	7	4	4	4	3	4	4
43.28 ± 1.56	33.07 ± 3.63	13.17* ± 1.51	43.77 ± 3.56	16.12 ± 0.40	7.10 ± 0.29	7.77 ± 0.26	8.38 ± 0.36
39.2–46.6	26.9*–46.0*	10.2*–15.4*	37.4–52.1	15.0–16.9	6.4–7.7	7.2–8.3	7.5–9.0
54	38	35	51	50	40	47	39
39.6	—	—	32.1	15.0	—	7.0	—
1			1	1		1	
42.2	—	—	37.8	15.84 ± 0.66	—	7.75	—
				14.5–16.8		7.4–8.1	
1			1	15		2	
38.67 ± 1.67	22.90 ± 2.64	19.64 ± 1.80	36.22 ± 3.89	14.40 ± 0.56	6.82 ± 0.38	7.08 ± 0.21	7.82 ± 0.43
36.1–41.4	19.2–27.9	17.3–23.1	29.4–43.6	13.3–15.1	6.2–7.3	6.8–7.5	7.0–8.6
13	9	11	13	14	11	12	12
44.67*	55.6*	11.0*	31.5	17.3	8.6	8.60	9.6
42.6*–47.2						8.5–8.7	
3	1	1	1	1	1	2	1
44.67*	55.6*	11.0*	31.5	17.83	8.70	8.62	9.80
42.6*–47.2				17.3–18.6	8.6–8.8	8.4–9.0	9.6–10.2
3	1	1	1	3	2	5	3

[a] Based on at least one measurement of Martin and Tate 1970; [b] based on different individuals (UNSM 20036, 20038); [c] from measurements of Marsh 1872; [d] may include one or more specimens which represent females.

* Slightly damaged specimen.

LATE PLEISTOCENE AND HOLOCENE TURKEYS IN THE SOUTHWEST

By Amadeo M. Rea[1]

ABSTRACT: Late Quaternary turkey remains from 17 southwestern sites are analyzed. All pre-agricultural turkeys, except those from northern Sonora and one cave in southern New Mexico, are found to be *Meleagris crassipes* L. Miller, an extinct species not closely related to the modern *M. gallopavo* Linnaeus, which inhabits much of the Southwest today. *M. gallopavo* is found associated with sedentary agriculturalists with a subsistence base of two or three crops at all other archaeological sites and time horizons. The major southwestern Indian cultures are herein delimited in time and space, emphasizing Mesoamerican components (particularly the four cultivars—maize, squash, gourd, beans—and macaws). It is proposed that the living turkey *M. g. merriami* Nelson is a parallel Mesoamerican component that was imported and became feral with the breakdown of southwestern cultures that had occurred by A.D. 1450, if not before.

It is currently believed that the Common Turkey, *Meleagris gallopavo* Linnaeus, occurred in the Southwest in the Pleistocene as well as the Holocene (=Recent) Epochs, evolving from local precursors (AOU 1957, Brodkorb 1964a; Schorger 1966; Steadman this vol.). The late Lyndon L. Hargrave long maintained (1970a:16, 25) that *M. g. merriami* Nelson, the subspecies of Common Turkey found today throughout most of the Southwest (Fig. 1), was derived from Pueblo Indian domesticated turkeys that became feral at the time of or following the breakdown and dispersal of the Anasazi Culture in the late thirteenth century. Hargrave's reasoning was that there were no Pleistocene or Pre-Basket Maker II cultural horizon Common Turkeys known from the Southwest. The independent discovery by Storrs Olson of the National Museum of Natural History, Smithsonian Institution, and by me, of the quite distinct paleospecies *Meleagris crassipes* L. Miller, in cave deposits in New Mexico, provided an opportunity to test Hargrave's hypothesis. Dr. Olson kindly placed the cave materials he was studying at my disposal because of the cultural (ethnobiological) ramifications of this problem. To resolve the question of the origin of *M. gallopavo,* a re-examination of all reputed pre-agricultural specimens of *M. gallopavo* throughout the range of modern *M. g. merriami* was necessary, particularly since both Olson and I found both *M. crassipes* and *M. gallopavo,* in the same cave deposits.

In this paper I shall attempt to present arguments that will provide answers to the following questions: (1) What were the geographic and temporal ranges of *M. crassipes* and *M. gallopavo* in the Southwest? (2) When did *M. crassipes* become extinct? (3) What was the relationship between the evolution of sedentary agricultural people and the domestication of the turkey in the area? (4) Did Puebloan peoples capture and domesticate birds from preexisting local wild populations, or were domestic turkeys imported along with Mesoamerican cultigens (maize, beans, pumpkins) and the macaw?

On the basis of the examination of existing fossil and archaeological remains, the first two questions can be answered with some degree of certitude, though carefully dated, stratified excavations might modify these answers. The third question will be sketched only in its broadest outlines, with the details left to the study by Charmion R. McKusick (this vol.). The final question cannot be answered directly, but a suggestion can be offered on the basis of available remains.

MATERIALS AND METHODS

Fossil and modern specimens cited in this report are distinguished by the following initials: AMNH (American Museum of Natural History), AMR (A.M. Rea Collection), FM (Field Museum), LACM (Natural History Museum of Los Angeles County), LLH (L.L. Hargrave Collection, Museum of Northern Arizona), MALB (Museum of Arid Land Biology, University of Texas, El Paso), MWU (Midwestern University), SC (Stanton's Cave, Museum of Northern Arizona), SD (San Diego Natural History Museum), TMM (Texas Memorial Museum, University of Texas, Austin), UA (Department of Ecology, University of Arizona), UAPL (Paleontology Laboratory, University of Arizona), USNM (National Museum of Natural History, Smithsonian Institution), and WAC (Western Archeological Center, Tucson).

All fossil and archaeological specimens were compared with the type series of *M. crassipes* (LACM), *M. californica* (LACM), and Recent wild *M. gallopavo* (total 31; *M. g. merriami, M. g. intermedia* Sennett, and *M. g. silvestris* Vieillot; AMR, UA, SD, LLH). Most of the cave material is not mineralized, except where noted. For identifications I used both qualitative and quantitative characters with a heavier reliance

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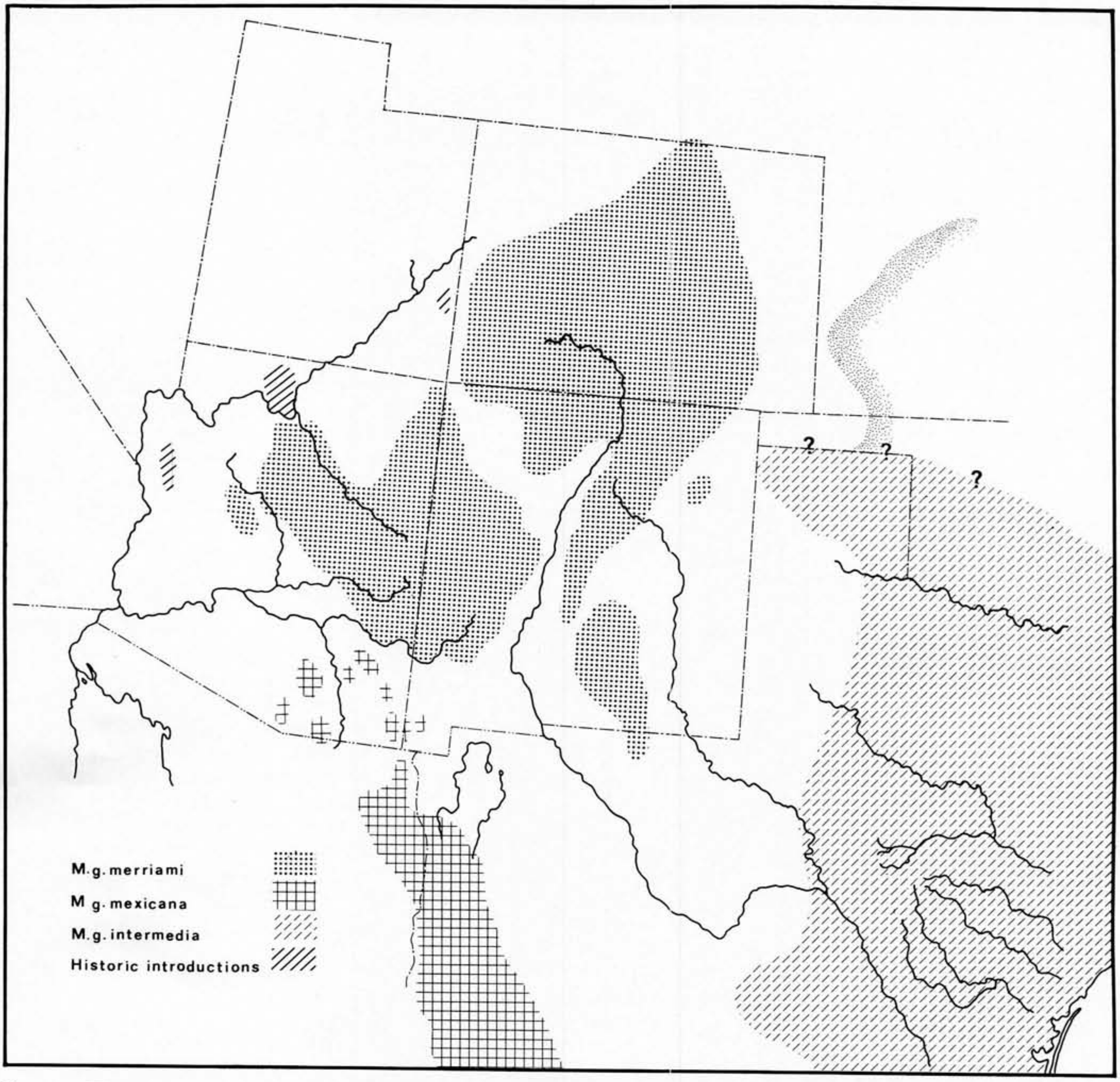

Figure 1. Historic (19th–20th Century) distributions of southwestern subspecies of *Meleagris gallopavo*. After European settlement, native turkeys were extirpated from the border ranges of southeast Arizona, and the areas were restocked with *M. g. merriami* starting early this century. Some forested areas of Utah and northwest Arizona, lacking historic populations, have been stocked with *M. g. merriami*. The Colorado and New Mexico range has been greatly reduced. (After Aldrich and Duvall 1955; Bailey 1929; Bailey and Neidrach 1965; Phillips et al. 1964; Schorger 1966; and other sources.)

on qualitative differences between the two species where possible. Most qualitative characters are given by Steadman (this vol.), although a few additional characters are mentioned below. Osteometric data are also given by Steadman (this vol.). Radiocarbon dates are followed by the standard deviation, with the laboratory and sample number in parentheses. All measurements are in millimeters. I have used two systems of dating throughout: years before present (B.P.) for dates older than 2000, and A.D. designations of the Gregorian calendar for those younger. Paleontologists more frequently use the former, prehistorians the latter. Breaking at A.D. 1/2000 B.P. appears to be the least awkward compromise.

SYSTEMATICS

Meleagris crassipes has been known since its discovery and description (Miller 1940, 1943) only from San Josecito Cavern in southern Nuevo León, México, on the east flank of the Sierra Madre Oriental. The species is represented by over 50 elements, mostly limb bones. The scapula, one character of which is most important in the evolutionary history of turkeys (Steadman this vol.), is unknown. The associated fauna of San Josecito Cavern includes the Rancholabrean land mammals *Canis dirus*, *Nothrotherium* sp., *Equus* sp., *Tetrameryx* sp., *Felix atrox*, and *Smilodon* sp. Extinct birds include *Coragyps occidentalis* (L. Miller) (=*C. atratus*? (Bechstein)), *Teratornis merriami* L. Miller, *Spizaetus grinnelli* (L. Miller), *Neogyps errans* L. Miller, *Neophrontops americanus* L. Miller, *Wetmoregyps daggetti* (L. Miller), and *Polyborus prelutosus* Howard (Miller 1943). *Meleagris crassipes* is a distinctive species, showing little similarity to the two living species of turkeys, *M. gallopavo* and *M. ocellata* Cuvier, or to their immediate precursors. Instead, it appears to have been a dead-end side branch in the evolutionary history of turkeys (Steadman this vol.). *M. crassipes* was a small turkey with relatively large legs, and little sexual dimorphism in size. San Josecito Cavern had surface evidence of human occupancy, but all the bird bones were recovered from "below the zone of human activity" (Miller 1943:144).

I am convinced that the osteological and external differences between the two living species of turkeys are insufficient to warrant placing them into separate monotypic genera, *Agriocharis* Chapman and *Meleagris* Linnaeus. The supposed generic characters are almost exclusively a matter of secondary sexual characteristics, such as the position, angle, and length of metatarsal spur, and the male head and chest ornamentation. The structure and color pattern of the wing, mantle, rump, and breast feathers of the two living species are strikingly similar. Osteologically, Holocene *M. gallopavo* and *M. ocellata* more closely resemble each other than either does *M. crassipes*. Ridgway (*in* Ridgway and Friedmann 1946:458) noted, "*Agriocharis* is, in fact, so closely related to *Meleagris* that I am somewhat doubtful as to the expediency of recognizing it as a genus." Brodkorb (1964a, b) removed the fossil species *M. leopoldi* A. Miller and Bowman and *M. crassipes* from *Meleagris*, leaving in that genus the three species *M. alta* Marsh, *M. tridens* Wetmore, and *M. gallopavo* Linnaeus. I regard *Agriocharis* as a synonym of *Meleagris*, thus returning the species *M. ocellata* Cuvier, *M. leopoldi* A.H. Miller and Bowman, and *M. crassipes* L.H. Miller to *Meleagris*, along with *M. progenes* (Brodkorb) and *M. anza* (Howard). I also strongly doubt that *M. californica* (L. Miller) is sufficiently distinct to merit being placed in the separate genus *Parapavo* L. Miller, and prefer considering it as well a species of *Meleagris*. Steadman (this vol.) has independently reached similar conclusions.

Finally, the so-called New World family Meleagrididae seems to me unjustifiable. The two living species and their paleo-antecedents are merely medium to large pheasants. I recommend placing them in the family Phasianidae, together with the spurred fowl of the Old World.

FOSSIL AND EARLY ARCHAEOLOGICAL RECORDS OF *MELEAGRIS* IN THE SOUTHWEST

STANTON'S CAVE, Coconino Co., Arizona. Grand Canyon, 51 river km below Lee's Ferry. Distal end of tarsometatarsus (SC 76). This bone was obtained from a packrat nest in the cave. Individual nests have not been dated, but the cave floor deposit ranges from 38,000 B.P. to present, with the bulk of the material being Pleistocene (Euler 1978). Bird bones recovered from the cave include *Teratornis merriami*, *Gymnogyps amplus* L. Miller (=*G. californianus*? Shaw), *G. californianus*, and *Centrocercus urophasianus* (Bonaparte). All of these species are absent from the area today. Mammals include *Oreamnos harringtoni* and *Bison* sp. The packrat nest was burned by vandals before the cave was excavated, so the tarsometatarsus is slightly calcined but not distorted. The specimen is clearly from *M. crassipes* on the basis of characters and lies within the upper size range of the specimens from San Josecito Cavern. The only evidence of human activity in Stanton's Cave was the presence of caches of split willow twig figurines, dated 3000–4000 B.P. (Euler 1978:158). The cave was never a habitation site.

LAGUNA SALADA, Apache Co., Arizona. Distal end of tibiotarsus (FM uncatalogued). Martin and Rinaldo (1960:115) reported the tibiotarsus of a turkey, *M. gallopavo*, taken at a playa camp site on the Upper Colorado, radiocarbon dated 3280 ± 60 (Gro. 1614) B.P. I have re-examined this bone and find it to be from a Sandhill Crane, *Grus canadensis* (Linnaeus). Certain bones of *Grus* and *Meleagris* are superficially similar (Hargrave and Emslie 1979).

PAPAGO SPRINGS CAVE, Santa Cruz Co., Arizona. Complete humerus (AMNH 8683, 8687); distal half of right humerus (AMNH 8693); proximal half of right femur (AMNH 8684); proximal two thirds of right femur (AMNH 2685); all mineralized. Steadman (pers. comm.) found these specimens indistinguishable from those of female *M. gallopavo* or male *M. crassipes*. I cleaned these fossils of some heavy matrix to expose critical characters for identification. The complete humerus is from *M. crassipes*. It differs from *M. gallopavo* in: much greater protrusion of head anconad, especially mediad; narrower capital groove; and very much smaller and differently shaped impression of M. brachialis anticus. Its length is about 121.8 mm. The scar of M. latissimus dorsi is not exposed. The partial humerus is from *M.* cf. *crassipes*. The impression of M. brachialis anticus is very short and broad, not extending up the shaft as in *M. gallopavo*. Its distal width is 26.5 mm. The femora are from *M. crassipes*. They differ from *M. gallopavo* in: very much wider neck, not pinched off; thicker ridge on posterior view separating trochanter from head and neck (2.5 mm vs. a fine line in equivalent-sized *M. gallopavo*); and general configuration of obdurator ridge area. The fauna of Papago Springs Cave is late Pleistocene, with abundant fossils of the extinct pronghorn, *Stockoceros onuscrosagris*, as well as *Camelops* sp., *Bison* sp., *Platygonus* sp., and two species of *Equus* (Skinner 1942).

NORTH PAPAGO (SONOITA) CAVE, Santa Cruz Co., Arizona. Complete tarsometatarsus lacking spur (AMNH 8686). This specimen is from *M. crassipes*. This cave is an extension of the above and is presumably the same age.

ARIZPE, Sonora, México. Río San Miguel drainage 97 km southeast of Cananea. Head of humerus (AMNH 6823), mineralized. This bone was identified by Cracraft (1968) as *M. gallopavo*. I can find no characters to distinguish it from a large male of that species. It is far too large (width of head, 38.9 mm) for *M. crassipes*, but it could be a very large *M. californica*. Steadman (this vol.) considers the character differences of the head of the humerus noted by Cracraft (1968) too inconsistent for a specific identification between *M. gallopavo* and *M. californica*. I refer the humerus to *M. gallopavo* on geographic probability. This deposit from northeastern Sonora yielded *Bison* cf. *alleni* and *Equus* cf. *tau,* suggesting a late Pleistocene age.

LA BRISCA, Sonora, México. Río San Miguel drainage about 25 km northwest of Arizpe. Distal end of ulna (IGCU-2546), mineralized. Size is not diagnostic in this specimen (distal width, 13.0 mm). Steadman's measurements (this vol., Tables 10, 11) indicate that the specimen lies within the size range of female *M. gallopavo,* female *M. californica,* or male *M. crassipes*. The ulna of *M. crassipes* is distinguishable from both *M. gallopavo* and *M. californica* on the basis of the shape of the internal condyle (short, almost squared in the former; broadly rounded in the latter two). The fossil ulna is the latter type. On the basis of this character and geographic probability I refer the La Brisca fossil to *M. gallopavo*.

TULAROSA CAVE, Catron Co., New Mexico. FM 73,2504 and 73,648, tarsometatarsi; 73,647, coracoid lacking part of head; 73,2247, head of coracoid; all from the pre-pottery occupational phase, radiocarbon dated 2300 (±200) to ca. 2150 years B.P. (Additional turkey bones recovered from younger cultural levels not re-examined.) All four elements are *M. gallopavo*. The tarsometatarsi are smaller and appear more gracile than in the wild female *M. g. merriami* living in the area today. The pathological coracohumeral surface of one coracoid suggests captivity.

SAN ANTONIO SITE, Socorro Co., New Mexico. Río Grande south of Socorro, 5.6 km NE San Antonio. USNM 14690: distal end of humerus; radius, lacking distal end; nearly complete ulna. Steadman (pers. comm.) examined these bones and could find no qualitative characters. Measurements are: humerus, distal width 23.8 mm; ulna: length 101.8+ mm, distal depth 12.3 mm; radius: proximal width 7.9 mm, proximal depth 8.3 mm. On the basis of measurements (Steadman this vol., Tables 8 through 13), I refer these specimens to *M. crassipes*. The fossils are from the base of a pumicite bed and there were no other associated bones. They are presumed to be Pleistocene, perhaps Blancan (Needham 1936).

HOWELL'S RIDGE CAVE, Grant Co., New Mexico. There have been three excavations of this cave deposit, two producing bones of *Meleagris*. Zeller-Howard pit: coracoid head (LACM 33890), scapula (LACM 33889), proximal and distal ends of an ulna (LACM 33891, 33892). Van Devender pit: tarsometatarsus, rodent gnawed on trochleae and most of head (SD uncataloged). No stratigraphic data were recorded on materials recovered from the Zeller-Howard pit, but Howard (1962) presumed that they were of late Pleistocene or Holocene age. Associated (Howard 1962) were *Equus* sp., *Camelops* sp., abundant *Gymnogyps amplus* (=*G. californianus*?) (including young), *Coragyps occidentalis* (=*C. atratus*?), and single elements of *Spizaetus* sp. and *Anabernicula* sp. Howard (1962:242) considered only the possibility that the turkey was either *M. gallopavo* or *M. californica*. She very tentatively referred the turkey elements to *M. gallopavo*. I identified the proximal end of the ulna (33891) as from *M. crassipes* on the basis of the short, distinctly squared shape of the internal condyle. After further cleaning of the head of the coracoid, I am inclined to consider it a specimen of *M. crassipes* rather than *M. gallopavo* or *M. californica* on the basis of the shape of the coracohumeral surface (broader, less triangular). The Howell's Ridge scapula has an almost obsolete foramen, unlike the known *M. gallopavo* and *M. californica* where the foramen is well developed, and it well may represent *M. crassipes*.

The large galliform bones recovered from the Harris pit (UTEP) are *Centrocercus urophasianus*. Van Devender (Van Devender and Worthington 1978) excavated additional parts of this cave with careful stratigraphic controls. Several large galliforms were obtained from the 90–100 cm level, midway between radiocarbon dates of 3330 ± 170 B.P. (A-1354) on the 70–80 cm level, and 6697 ± 324 B.P. (average of A-1429 and A-1430) on the 110–112 cm level. Both dates are based on endocarps of *Celtis reticulata* (netleaf hackberry). The 90–100 cm level includes the nearly complete and excellently preserved tarsometatarsus of *M. crassipes,* apparently a mature female (no evidence of spur attachment). The other galliforms from this stratum are *Centrocercus urophasianus*. Zeller (Howard 1962:241) suspected human association on the basis of a few flint chips and charcoal, but Van Devender and Harris (pers. comm.) found no suggestion of human occupation.

SHELTER CAVE, Doña Ana Co., New Mexico. Incomplete humerus (LACM 1010/653), two pedal phalanges (LACM 1010/657), distal ends of right and left ulnae (LACM 1010/556, 557). The humerus more closely resembles topotypes of *M. crassipes* than Hargrave's extensive series of *M. gallopavo merriami* in such characters as: (1) general greater curvature of the shaft; (2) size (least depth of shaft 9.4 mm); (3) very small brachial depression; and (4) small, slender depression for M. latissimus dorsi. The pedal phalanges cannot be identified to species. The ulnae are identical to those of *M. crassipes,* except one measures slightly larger (16.0 mm) than the largest of six ulnae (14.1 to 15.6 mm) of *M. crassipes* from San Josecito Cavern. Associated with these specimens are *Gymnogyps californianus*? and the extinct species *Urubitinga fragilis, Geococcyx conklingi* Howard, and *Pyelorhamphus molothroides* A. Miller, all indicating Late Pleistocene age, but with evidence of Basket-Maker-like (Archaic) material culture overlying the fore part of the cave (Howard and A. Miller 1933). This cave and the following are on the west and east sides, respectively, of Pyramid Peak in the southern Organ Mountains, north of El Paso, Texas.

CONKLING CAVERN, Doña Ana Co., New Mexico. Shaft of humerus (LACM 1009/21), carpometacarpus (LACM 1009/22), distal end of radius (LACM 1009/23). The humerus, from the 20–23 foot level, is far too large (least diameter of shaft, 11.9 mm; Steadman this vol., Tables 8, 9) and too straight for *M. crassipes,* but agrees with that of male *M. gallopavo*. The brachial depression is not deep, but its size and shape resemble those found in *M. gallopavo*. Surface striations indicate immaturity. The carpometacarpi of *M. crassipes* and *M. gallopavo* can be distinguished by the outer curvature of the distal end of metacarpal III, but this area is broken on specimen 1009/22. Measurements of the carpometacarpus are: proximal depth 23.4 mm, minimum axial length 75.6 mm, and maximum axial length (78.2+ mm). These measurements are all too large for *M. crassipes* and greater than the largest *M. californica* measured by Steadman (this vol., Tables 14, 15). Its provenience is marked "dump" (presumably material outside the cave disturbed by treasure hunters, lacking stratigraphic data). The radius, also lacking provenience data, measures 12.8 mm in distal width. I consider all three elements to be *M. gallopavo*. Associated specimens from Conkling Cavern are *Coragyps occidentalis* (=*C. atratus*?), *Gymnogyps californianus, Geococcyx conklingi,* as well as *Centrocercus urophasianus* and *Cyanocephalus cyanocephalus,* two species living today in more northern arid regions (Howard and Miller 1933). Mammals include extinct *Equus* sp., an ursid, *Hemiauchenia* sp., *Camelops* sp., and *Nothrotherium*. There were human remains (presumably Paleo-Indian) at the 10 and 21 foot levels, but no Late Archaic material culture. At the 20 foot level there was a hard, water-deposited, horizontal lens, precluding the possibility of intrusive burial (Bryan 1929). Howard and A. Miller (1933:17) consider the better stratified lower levels of Conkling Cavern to be Pleistocene.

DRY CAVE, Eddy Co., New Mexico. Guadalupe Mountains. Distal end of tarsometatarsus (trochlea gnawed by rodent) (MALB 5-239). This specimen of *M. crassipes* was excavated by A.H. Harris from the Sabertooth Camel Maze section of Dry Cave. The fossil remains are dated 25,160 ± 1730 B.P. This portion of the cavern was sealed so that it was not contaminated with younger materials (Harris pers. comm.). Associated animals include *Breagyps clarki, Canis dirus, Camelops* sp., *Tapirus* sp., and *Equus* sp.

BURNET CAVE, Eddy Co., New Mexico. East slope of Guadalupe Mountains, about 80 road km west of Carlsbad. Shaft of humerus (ANSP 14161); carpometacarpus (ANSP 13495); femur, lacking distal end (ANSP 14134); tarsometatarsus with spur (ANSP 13492); tibiotarsus, lacking proximal end (ANSP 14133). The upper 0.5 to 1 meter of the open cave deposit have Basket-Maker-like burials, but lack corn cobs and pottery (Schultz and E. Howard 1935:273–274). Beneath 1 meter, extending to a depth of 3 meters, were numerous hearths and "Folsom-like" artifacts associated with extinct mammals (*Bison antiquus, Preptoceras sinclairi, Stockoceros onusrosagris, Euceratherium collinum*) and the condor *Gymnogyps californianus*. The spurred tarsometatarsus and the carpometacarpus, both recovered in the 5 ft 9 in. stratum, are from *M. crassipes*. The femur (stratum unknown) also appears to be from *M. crassipes* (muscle lines and other characters) and is buff-tan colored like the previous two elements. The tibiotarsus (14133) is too large and too long for *M. crassipes* (width across distal cotyla 18.4 mm vs. maximum 17.4 mm in *M. crassipes*; distance from distal end of scar for attachment of fibula to distal end 122.7+ mm vs. maximum 104.3 mm in *M. crassipes*; Steadman this vol., Tables 18, 19). The shaft of the humerus (14161) is too straight and too large for *M. crassipes*. Both the tibiotarsus and humerus fit *M. gallopavo,* the humerus being in the size range of a male. These latter two bones, as Olson (pers. comm.) has pointed out, are quite white in color, in contrast to the brownish (and probably older) *M. crassipes* from this deposit. These two elements were presumably associated with the upper 0.5 meter of deposit containing Archaic cultural remains.

DARK CANYON CAVE, Eddy Co., New Mexico. About 25 km southwest of Carlsbad. Nearly complete coracoid (AMR, uncataloged). Howard (1971:237–240) reported on a large portion of this enormous deposit, although thousands of bird bones still remain to be identified. She reported two turkey bones, listing them as "*Meleagris gallopavo*?" These and certain other galliform bones were returned to the late L.L. Hargrave, and cannot now be found in his collection. The cave contained abundant teeth of *Equus* sp., and many extinct avian species, including *Anabernicula* sp., *Gymnogyps amplus* (=*G. californianus*?), *Coragyps occidentalis* (=*C. atratus*?), *Neophrontops* sp., *Geococcyx conklingi,* and others. The deposit containing the extinct species was overlain with Basket-Maker-like material culture.

A coracoid, lacking part of the sternal facet, was obtained during subsequent excavations at approximately the 15 foot level. The distinctive shape of the coracohumeral surface and additional characters mentioned by Steadman (this vol.) indicate that it is from *M. crassipes*. Measurements of the specimen are: head to internal distal angle 70.5 mm; head through scapular facet 26.3 mm; least width of shaft 7.6 mm. It was associated with the coracoid of *Gymnogyps* sp.

PRATT CAVE, Culberson Co., Texas. McKittrick Canyon, south of Carlsbad, Guadalupe Mountains. Fragmental distal end of humerus (WAC 38A1); fragmental distal end of shaft of tibiotarsus (WAC 35A1); distal end of tibiotarsus (WAC 2599/34A1). There is some question of the antiquity of this deposit. I have re-examined the extralimital pigeon, *Columba flavirostris* Wagler (distal end of humerus), and the extinct roadrunner, *Geococcyx conklingi* (proximal end of tibiotarsus), identified from the deposit by Hargrave. I find the humeri of *C. flavirostris* and *C. fasciata* Say, the species of pigeon to be expected at the site, to be indistinguishable, even using the comparative materials from the Hargrave Collection (all the *C. flavirostris* specimens being from captive birds). The bone from Pratt Cave is undoubtedly *C. fasciata*. Rob McKenzie and I have compared the roadrunner tibiotarsus with the type series (LACM) of Conkling's Roadrunner, finding that it indeed appears to be *G. conklingi,* though it is slightly larger and somewhat different in characters. This cave lacks an extinct megafauna, and the herpetofauna is also modern. The entire deposit appears to be less than 6000 B.P. (Gehlbach and Holman 1974:191, 195). The late Archaic remains are radiocarbon dated 2320 ± 70 to 1420 ± 60 B.P. A. Schroeder (pers. comm.) provided stratigraphic data on the cave showing that all the turkey bones are from cultural levels in the cave. The fragmentary humerus is the size of a large male *M. gallopavo* (depth through internal condyle 12.5 mm; depth through external condyle 27.6 mm). The shaft of a tibiotarsus is immature and burned at the distal end. It cannot be identified to species. The distal end of tibiotarsus from a test pit is the size of a large female *M. gallopavo*. Steadman (this vol.) finds no diagnostic characters in distal ends of tibiotarsi.

LUBBOCK LAKE, Lubbock Co., Texas. Llano Estacado (southern High Plains), north of the Edwards Plateau. Restored fragments of distal end of tibiotarsus (TTU-A1399) and humerus (TTU-A1391); two pedal phalanges (TTU-A1390, 1443). These several fragmentary elements, from the same horizon in a Clovis Man level, are referred to a single individual. They are not identifiable to species. The date is late Pleistocene (12,000–11,000 B.P.). The associated megafauna includes *Mammuthus* sp., *Equus* sp., *Camelops* sp., *Bison* sp., and *Tapirus* sp. (Johnson 1977:65).

KLEIN CAVE, Kerr Co., Texas. South-central Texas, northwest of San Antonio. Distal end of femur (MWU 9110). The cave deposit is dated at 8000 B.P. (Roth 1972). The lack of an extinct megafauna is attributed to the shallowness of the cave (Roth 1972:77). Mammals from the cave that require a mesic habitat and are no longer found on the Edwards Plateau

Table 1. Late Pleistocene and early Holocene paleontological remains from the southwest.

Cave, Location	Species	Element	Provenience	Association	Age	Original Source
STANTON'S CAVE Coconino Co., Ariz.	*Meleagris crassipes*	tarsometatarsus	packrat midden	*Teratornis*, *Gymnogyps*, modern fauna	38,000 B.P. to Recent	Rea and Hargrave MS
LAGUNA SALADA Apache Co., Ariz.	*Grus canadensis*	tibiotarsus	camp site	cultural	3280 ± 60 B.P.	Martin and Rinaldo 1960
PAPAGO SPGS. CAVE Santa Cruz Co., Ariz.	*M. crassipes* *M.* cf. *crassipes* *M. crassipes*	humerus humerus 2 femora	none	Pleistocene megafauna	Late Pleistocene	Skinner 1942
NORTH PAPAGO CAVE Santa Cruz Co., Ariz.	*M. crassipes*	tarsometatarsus	none	Pleistocene megafauna	Late Pleistocene	
ARIZPE Sonora, México	*M.* cf. *gallopavo*	humerus head	none	*Bison*, *Equus*	Late Pleistocene	Cracraft 1968
LA BRISCA Sonora, México	*M.* cf. *gallopavo*	ulna	surface	*Strix brea*, *Equus*	Late Pleistocene	
TULAROSA CAVE Catron Co., N. Mex.	*M. gallopavo*	2 tarsometatarsi 2 coracoids	pre-pottery level	cultural	2300–2150 B.P.	Martin et al. 1952
SAN ANTONIO SITE Socorro Co., N. Mex.	*M.* cf. *crassipes*	humerus ulna radius	base of pumicite bed	none	Early? Pleistocene	Needham 1936
HOWELL'S RIDGE CAVE Grant Co., N. Mex.	*M. crassipes* *M. crassipes?* *M. crassipes*	ulna scapula coracoid	none (Zeller-Howard pit)	*Equus*, *Camelops*, *Gymnogyps*, *Coragyps*, *Spizaetos*	presumed late Pleistocene	Howard 1962
	M. crassipes	tarsometatarsus	90–100 cm level	*Centrocercus urophasianus*	3330–6697 B.P.	Van Devender and Worthington 1978
SHELTER CAVE Doña Ana Co., N. Mex.	*M. crassipes* *M. crassipes*	humerus 2 ulnae	none	*Gymnogyps*, *Pyelorhamphus*, *Geococcyx conklingi*	Late Pleistocene to Late Archaic "Basket Maker"	Howard and A. Miller 1933
LUBBOCK LAKE Lubbock Co., Texas	*Meleagris* sp.	tibiotarsus humerus fragments	Clovis Man level	*Mammuthus*, *Tapirus*, *Equus*, *Camelops*	12,000–11,000 B.P.	Johnson 1977, Rea in press
KLEIN CAVE Kerr Co., Texas	*M. gallopavo*	femur	?	*Synaptomys cooperi*, *Mustela erminea*, *Tamias striatus*	8000 B.P. (noncultural)	Roth 1972, Feduccia 1972
SAN JOSECITO CAVERN Nuevo León, México	*M. crassipes*	>50 elements	below cultural zone	*Teratornis*, *Gymnogyps*, *Smilodon*, *Tetrameryx*, *Equus*, *Nothrotherium*	Late Pleistocene	Miller 1943
INGLESIDE PIT San Patricio Co., Texas	*M. gallopavo*	3 tibiotarsi 2 tarsometatarsi 1 coracoid		*Ciconia maltha*, *Gopherus hexagonata*, *Geochelone*, *Mammuthus*, *Mammut*, *Camelops*	Late Pleistocene	Feduccia 1973, Steadman (this vol.), Lundelius 1972
CONKLING CAVERN Doña Ana Co., N. Mex.	*M. gallopavo* *M. gallopavo*	radius humerus shaft	none 6 to 7 m level	*Coragyps*, *Gymnogyps*, *Camelops*, *Equus*	Paleo-Indian 13,000–9000 B.P.	Howard and A. Miller 1933
	M. gallopavo	carpometacarpus	"dump"			

Table 1. Continued.

Cave, Location	Species	Element	Provenience	Association	Age	Original Source
DRY CAVE Eddy Co., N. Mex.	*M. crassipes*	tarsometatarsus		*Breagyps, Canis dirus, Camelops, Tapirus, Equus*	25,000 B.P.	Harris 1978
BURNET CAVE Eddy Co., N. Mex.	*M. crassipes*	tarsometatarsus	5′9″ (1.75 m)	Folsom-like artifacts; *Bison, Tetrameryx, Gymnogyps*	Late Pleistocene	Schultz and E. Howard 1935, Wetmore 1932
	M. crassipes	carpometacarpus				
	M. crassipes	femur				
	M. gallopavo	tibiotarsus	none (upper 0.5 m?)	presumably Late Archaic		
	M. gallopavo	humerus				
DARK CANYON CAVE Eddy Co., N. Mex.	? (lost)	unknown (2)	unknown	*Gymnogyps, Coragyps, Anabernicula, Neophrontops, Equus*	Late Pleistocene	Howard 1971
	M. crassipes	coracoid	4.5 m, new pocket	*Gymnogyps, Equus*	Late Pleistocene	
PRATT CAVE MKA-1 Eddy Co., N. Mex.	*M. gallopavo* *Meleagris* sp.	humerus tibiotarsi	cultural	*Geococcyx conklingi*, and modern fauna, Late Archaic	2320–1420 B.P.	Unpublished report

include *Tamias striatus, Microtus pennsylvanicus, Synaptomys cooperi, Mustela erminea, Myotis lucifugus,* and *Myotis evotis*. This indicates a climatic shift from cool, moist conditions to warm, dry conditions on the plateau. Roth (1972) found no evidence of human habitation in Klein Cave. Feduccia (1972) identified the distal end of a femur as *M. gallopavo* within the size range of a female. Steadman (this vol.) considers the depth of the intercondylar fossa to be a diagnostic character between *M. crassipes* and *M. gallopavo,* and we could not distinguish the Klein Cave specimen from three recent wild female *M. gallopavo* at hand. This is the westernmost specimen of *M. gallopavo* from the late Pleistocene/early Holocene, exclusive of Sonora and southwest New Mexico, not directly associated with man.

INGLESIDE PIT, San Patricio Co., Texas. About 1.5 km inland from the Gulf of Mexico. Feduccia (1973:143) reported six bones (all mineralized): coracoid (TMM 30967-1741), tibiotarsi (TMM 30967-1139, 30967-1063B, 30967-1564), tarsometatarsi (TMM 30967-1169, 30967-1467) as *M. gallopavo*. Steadman (this vol.) has re-examined the material and agrees with Feduccia's identification. The fauna is late Pleistocene.

In summary, this critical evaluation of turkey remains from the Southwest (Table 1; Fig. 3) shows that *M. crassipes* was widespread from Nuevo León, México, to the Grand Canyon, Arizona, in the late Pleistocene. In most caves it is associated with other extinct birds and Rancholabrean land mammals. The earliest radiocarbon date for *M. crassipes* is 25,000 B.P. (Dry Cave, New Mexico), and it persisted at least until some time between 3300 and 6600 B.P. (Howell's Ridge Cave, New Mexico). Its presence in greater numbers in southern New Mexico reflects the large number of cave deposits with bones of smaller vertebrates in that area. *M. crassipes* does not appear temporally sympatric with *M. gallopavo* in any deposit. So far there is no direct evidence that early man played a role in the extinction of this medium-sized turkey.

The late Pleistocene to early Holocene turkey specimens referred to *M. gallopavo* are restricted to southern New Mexico (Conkling Cavern), northern Sonora (Arizpe, La Brisca), the south-central and Gulf portions of Texas (Klein Cave and Ingleside Pit), and points east (Steadman this vol.). Throughout the remainder of the Southwest, *M. gallopavo* occurs only after Paleo-Indian times in association with the remains of sedentary agriculturalists.

There are three hypotheses that might explain the unusual distributions of the two turkey species from the Southwest:

1. *M. crassipes* and *M. gallopavo* occurred sympatrically in the Southwest from the late Pleistocene onward, but only *M. crassipes* was taken into caves by predators; *M. crassipes* became extinct, but *M. gallopavo* persisted. I consider differential predation unlikely. The male of *M. crassipes* was as large as a female *M. gallopavo*. If both species were present there should have been an equal chance of either species being deposited in caves by predators.

2. *M. crassipes* was the only turkey present in the Southwest. When it became extinct *M. gallopavo* extended its range from the east or the south to fill the vacated area. There is nothing intrinsically wrong with this hypothesis and it cannot be proven or disproven. However, climatic factors would seem to discredit the idea of a natural invasion by this large and relatively sedentary species. During the Holocene the Southwest underwent a general trend toward a warmer, dryer climate, with woodlands giving way to grasslands and deserts and xeric-adapted plants from México migrating northward at about the time *M. gallopavo* would have been invading (Van Devender 1976, 1977; Van Devender and Wiseman 1977; Wells 1966; Wells and Berger 1967). Forests became more and more restricted to mountain islands in the Southwest and the

juniper-piñon-oak woodlands retreated upslope 260 to 1000 meters (Van Devender and Spaulding 1979). The modern species of turkey would have been invading as its preferred habitat of woodlands was shrinking.

3. A third hypothesis is that (a) only *M. crassipes* occupied the niche of a large phasianid bird during the late Pleistocene, but became extinct during the Holocene; (b) man imported *M. gallopavo,* along with other domesticated plants and animals; (c) these turkeys escaped, forming a feral population north of *M. g. mexicana* and west of *M. g. intermedia*. Any serious consideration of this hypothesis requires a look at the evolution of sedentary cultures in the Southwest, the development of Mesoamerican cultivars, the development of trade routes between Mesoamerica and the Southwest, the transmission of cultural items, and finally, the present distribution and characteristics of the various subspecies of *M. gallopavo*.

THE EVOLUTION OF SEDENTARY CULTURES IN THE SOUTHWEST

PALEO-INDIANS AND DESERT CULTURE

The waves of early man sweeping across the North American continent from Asia are called Paleo-Indians. These cultures are usually characterized by their distinctive lithic artifacts; Clovis and Folsom people are well-known examples. Paleo-Indians are usually characterized as megafauna (big game) hunters who exploited many now extinct mammal species, beginning sometime between 15,000 and 10,000 B.P. They also hunted smaller game (Jennings 1974:90–92; Johnson 1977). The somewhat younger Desert Culture of the Archaic stage not only included the Southwest and Great Basin (McGregor 1965:124–125) but extended from southeast Oregon to the Valley of México (Martin and Plog 1973:69). The Cochise Complex, a part of this widespread Desert Culture, occupied much of the arid Southwest, lasting in places as late as 2000 B.P. Regardless of the names and times, these cultures, until at least late Cochise times (Dick 1965:100; Martin and Schoenwetter 1960:33–34), were pre-ceramic and pre-agricultural, dependent entirely on hunting and gathering (especially seeds) for subsistence.

ANASAZI CULTURE (COLORADO PLATEAU)

Some knowledge of three subsequent cultures, the Anasazi, Mogollon, and the Hohokam (Fig. 2) are critical to understanding the pre-history of *M. gallopavo* in the Southwest. The Archaic phenomenon was a general cultural stage that spread across North America from 8–9000 to 2–4000 B.P. It was best developed in the Southwest (or at least is best known there because of the circumstances of preservation in this arid region) (Amsden 1949; A. Morris 1933:39–55; McGregor 1965:170–186; 206–217; Wormington 1978:27–57; Jennings 1974:134; Martin and Plog 1973:81). The late Archaic San Juan peoples from the Anasazi or Four Corners region (San Juan and Little Colorado drainages) developed through several cultural stages (Basket Maker II and III; Pueblo I through IV), ending in the post-conquest pueblos of today such as Hopi, Acoma, and Zuni. (The cultural stage Basket Maker I is a hypothetical proto-agricultural stage that has not been discovered.)

Basket Maker II people, dating approximately A.D. 300–500 (McGregor 1965:471) are characterized by finely woven sandals and other textiles, atlatls for hunting, and corn/squash agriculture. The turkey appears in deposits from this time period *only* as feathers or feathered artifacts (Hargrave 1970a; Emslie and Hargrave 1978), not as bones. Toward the end of Basket Maker III time (McGregor [1965:215] puts this around A.D. 600–700), the turkey was certainly domesticated in the regions occupied by the Anasazi and evidence of whole turkey skeletons (almost never individual elements) appears (A. Morris 1933:196–197; E. Morris 1939:120). At approximately the same time, Basket Maker III culture underwent three critical advances, one technical (development of fired pottery), and two agricultural (introduction of beans [*Phaseolus* sp.] and the appearance of newer and larger varieties of corn [*Zea mays*]). The bow and arrow appeared about this time (Amsden 1949:133; Wormington 1978:55) or somewhat earlier.

Early Basket Makers used mammal fur cordage for twining blankets and for clothing. Later in the culture, feathers, particularly from turkeys, were used for this purpose (Hough 1914:5–6, 71–73; Wormington 1978:55, 89; A. Morris 1933:197; Amsden 1949; McGregor 1965:181, 215; Lange 1950.) Amsden pointed out that the fur-cord robes were astonishingly heavy but that turkey-feather material had the advantage of lightness. At this time turkey feathers were also starting to be used for ceremonial purposes. The intensive use of turkey feathers continues in the complex religious ceremonies of today's Pueblo Indians.

Pueblo II and III peoples had their greatest expansion between A.D. 900 and 1100 (see map, McGregor 1965:279). There is evidence (turkey bone awls and individual elements, occasionally charred, disposed of in trash mounds) that, beginning in this period, the turkey was used for food, at least locally. But at earlier sites of these peoples only whole birds occur as carefully interred burials (A. Morris 1933:196–197; Reed 1951:197, 200–201; McKusick this vol.). Stiger (1979:140) hypothesizes the use of turkeys for grasshopper control by Pueblo III times.

Compared to the adjacent Mogollon Culture, the Anasazi were late in overall cultural development. In the acquisition of genetic materials whose ultimate origin was Mesoamerica, they were centuries behind (see discussion beyond and Table 2).

An exceptionally early Anasazi turkey (*M. gallopavo*) is a mummy from Canyon del Muerto in Canyon de Chelly, estimated to date to A.D. 250 (Schorger 1961, 1966:20, 1970). It is from a race unknown in the wild. McKusick (pers. comm.) believes the dating is correct.

Turkey bones are found in late Archaic Basket-Maker-like deposits from southern New Mexico (Burnet Cave, Pratt Cave, and perhaps the dump material from Conkling Cavern). Presumably these people had a good agricultural base and were capable of maintaining captive turkeys, but little ethnobiological material was salvaged from these earlier excavations.

MOGOLLON CULTURE (MOUNTAINS)

Evidence for the domestication and use of turkeys in the mountainous areas of the Southwest occupied by the Mogollon peoples (Fig. 2) is equivocal. Reed (1951:202) states categorically that "the turkey was certainly not domesticated or

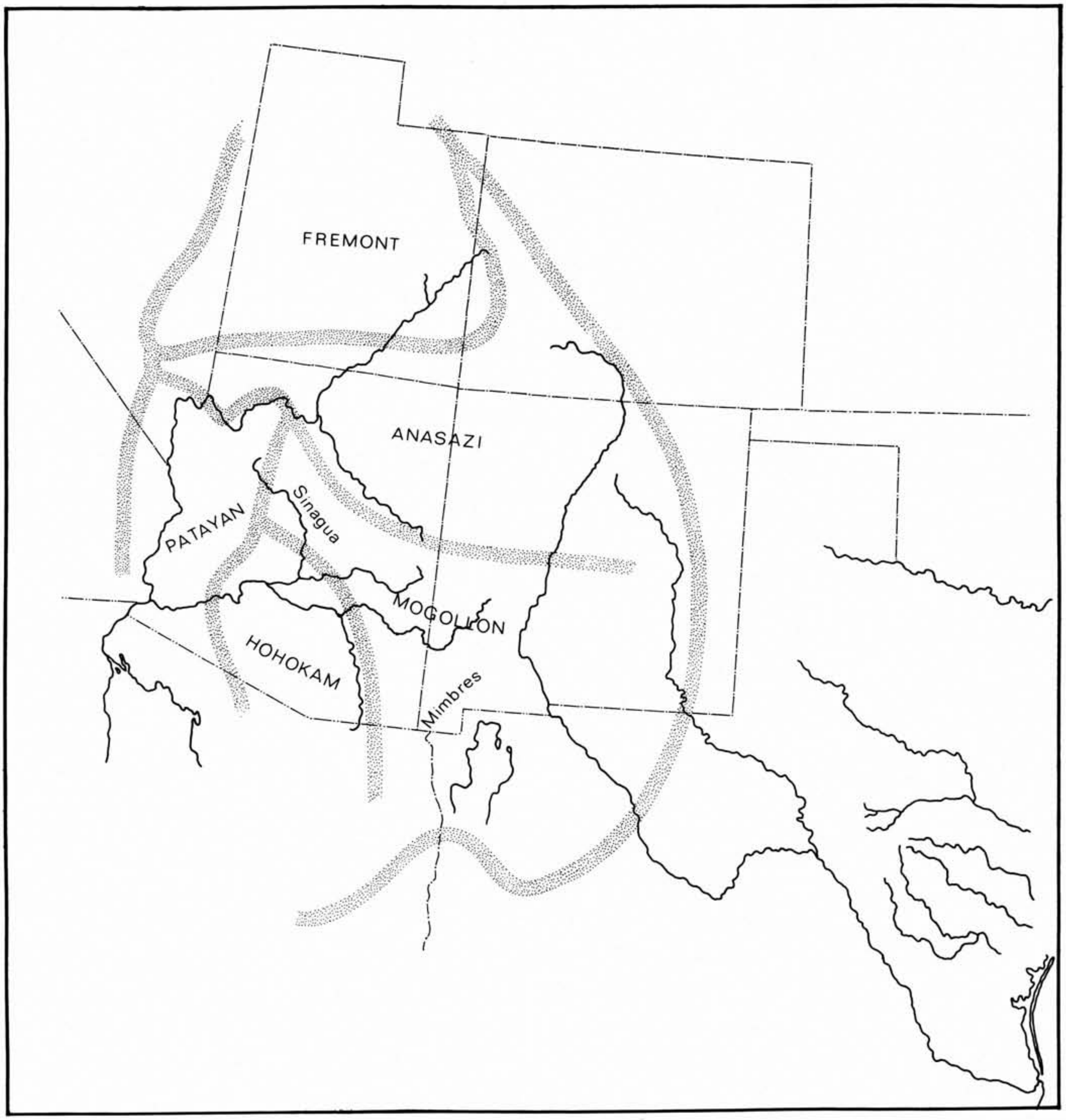

Figure 2. Generalized southwestern cultural areas, ca. A.D. 700–1100. (Modified from various sources.) Four major cultural areas are shown. The Mimbres is a late local development of Mogollon Culture. The Sinagua sub-area resulted from influences of Anasazi, Hohokam, and Mogollon. Also late was a Puebloid influenced sub-culture (not shown) along the Hohokam-Mogollon interface, often considered a distinct culture, the Salado.

kept by the Mogollon Pueblo groups of the forested uplands." (Such statements rely heavily on the presumption that wild turkeys were available; e.g., Haury 1936:93.) However, turkeys clearly were being raised in Tularosa Cave where Hough (1914:5) reported finding desiccated chicks, eggs, and great quantities of droppings. Schorger (1961) reported finding the crop of an adult mummy filled with a variety of colored flint corn grown by the Mogollon people between A.D. 500 and 700. Martin et al. (1952:499) noted that turkeys appear in the Mogollon record (Pine Lawn Phase, 2150 B.P. to A.D. 500) several centuries earlier than in the Anasazi area.

The oldest evidence for a primitive maize north of México is from Bat Cave, Catron Co., New Mexico, at levels even older than the Mogollon Culture (Dick 1965:100). This is a

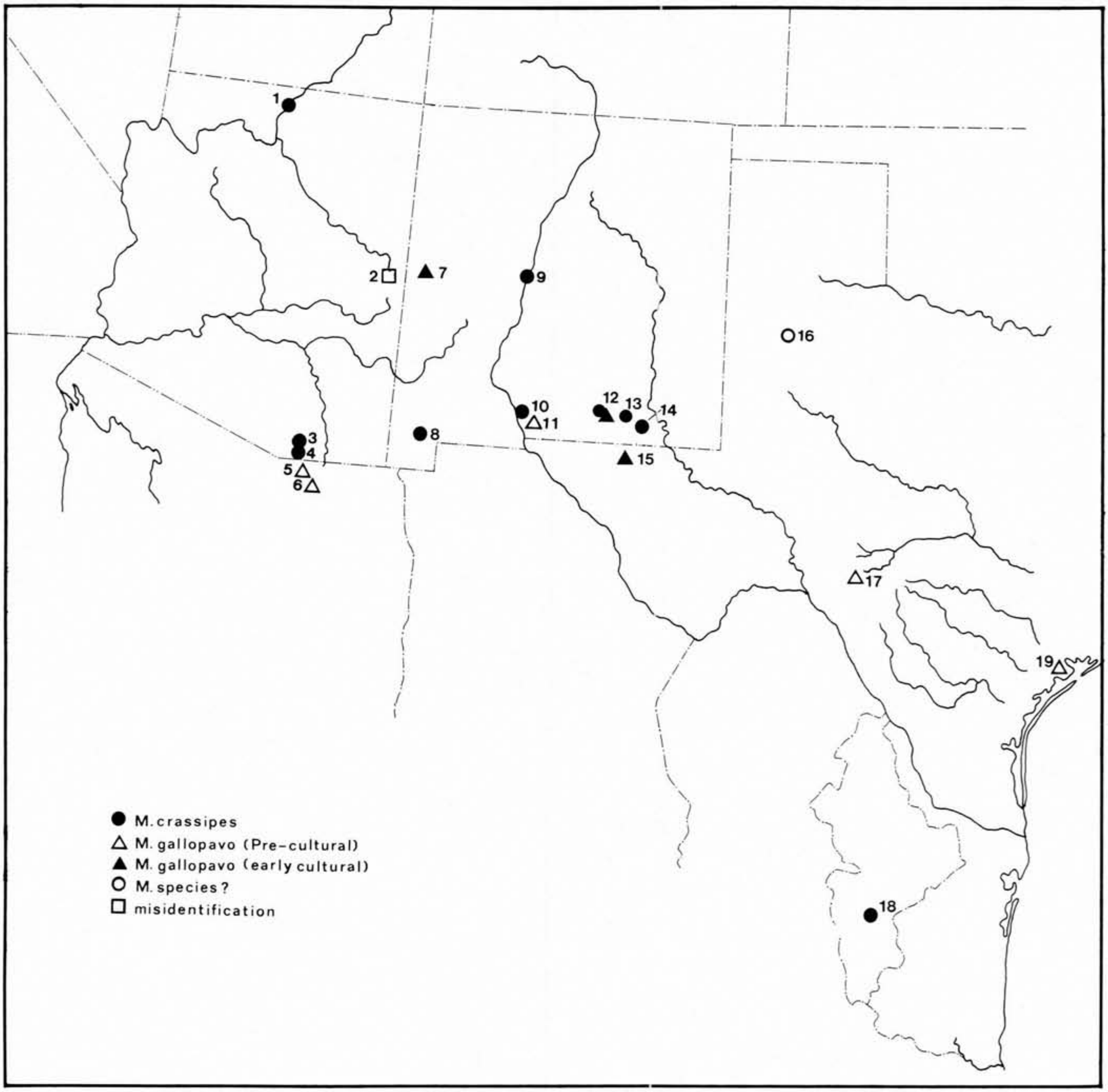

Figure 3. Localities where fossil to early cultural *Meleagris* bones have been reported from the Southwest. See Steadman (this vol.) for details on San Josecito Cavern and Ingleside Pit. 1, Stanton's Cave. 2, Laguna Salada. 3, North Papago Cave. 4, Papago Springs Cave. 5, La Brisca. 6, Arizpe. 7, Tularosa Cave. 8, Howell's Ridge Cave. 9, San Antonio Site. 10, Shelter Cave. 11, Conkling Cavern. 12, Burnet Cave. 13, Dry Cave. 14, Dark Canyon Cave. 15, Pratt Cave. 16, Lubbock Lake. 17, Klein Cave. 18, San Josecito Cavern. 19, Ingleside Pit.

pod popcorn brought into the Southwest as a *cultivated* variety, presumably from the south at least by 5500 B.P. (Dick 1965:93; Mangelsdorf 1954:409). There is a continuous and copious record of corn and its varietal progression in Bat Cave. Abundant vertebrate bones were recovered, but the bird and smaller mammal bones are still unanalyzed (Dick pers. comm.). In nearby Tularosa Cave, a primitive pod corn appears around 2000 B.P. Pottery and turkey feathers also occur about this time, their earliest occurrence in the Southwest. Some caves produced large numbers of turkey bones (Martin and Rinaldo 1950:492; Martin et al. 1952:204, 1954:155), others few or none. The presence of very few turkey bones from Mimbres sites (sometimes considered a separate culture, A.D. 700–1150) has been interpreted as absence of the bird as a domesticate. However, Mimbres people were familiar with the bird and painted it realistically on pottery.

HOHOKAM (SONORAN DESERT)

Paralleling in time the early Basket Maker developments to the north was the Hohokam Culture in the Lower Sonoran Desert regions of southern Arizona. Like the Mogollon Cul-

Table 2. Comparison of subspecific characters of male Common Turkey, *Meleagris gallopavo.*[1]

Subspecies	Rectrix Tips	Upper Tail Coverts	Rump	Size[2]
M. g. merriami	buff or grayish white	buff to white	bluish-black	large
M. g. gallopavo	white	pale pinkish buff to white	blue-black	medium
M. g. mexicana	white	pinkish white	coppery and greenish	large
Eastern races[3]	cinnamon to chestnut	dark chestnut	glossy black (*intermedia*)	variable (large to small)

[1] After Schorger (1966) and Ridgway and Friedmann (1946).

[2] As determined by wing measurements given in Ridgway and Friedmann (1946); there is relatively little size difference between the tarsometatarsi of these subspecies (means of males range from 162 to 173.8 mm). Sample sizes are small, ranging from 1 to 11. Osteological measurements should be more indicative of actual body size of subspecies.

[3] *M. g. sylvestris, M. g. osceola,* and *M. g. intermedia.* These three subspecies are richly colored, dark-rumped races.

ture, the Hohokam had corn agriculture and ceramics by at least 2000 B.P. (Ventana Cave, Haury 1950:164–165; Snaketown, Haury 1976:117–118; Cutler and Blake 1976:365–366; Bohrer 1970), as well as an elaborate water control technology.

Turkey bones are virtually or completely absent from Hohokam sites. Several reputed bones require verification, but Haury (pers. comm.) has been unable to relocate the remains reported from the first Snaketown excavation (Haury 1937:156). The second, more thorough excavation produced no turkey bones (McKusick 1976). A supposed turkey bone necklace (Arizona State Museum, Carpenter 1977) from a San Pedro site proves to be lagomorph long bones (pers. obs.). I have identified a coracoid of a female-sized Small Indian Domestic from the Las Colinas Site (Phoenix, Arizona) that is too small and gracile for either a wild *M. g. merriami* or an intrusive barnyard female. However, it dates from the late period of Salado-Publoid intrusion, A.D. 1180–1450. I know of no good evidence of any turkey element from a pure Hohokam horizon (i.e., one without Salado cultural influence).

ORIGINS AND DEVELOPMENT OF MESOAMERICAN CULTIVARS

At least five Mesoamerican domesticates or semi-domesticates are known to have entered southwestern cultures by diffusion or direct trade. These are corn, squash of several species, gourds, beans of several species, cotton, and macaws. Another animal domesticate, the dog, *Canis familiaris,* is more ancient, and probably of Old World origin. It is known from late Archaic times (4500 B.P. at Ventana Cave, Haury 1950:158; beginning of Snaketown, Haury 1976:115, 120; from the beginning of Basket Maker II, Amsden 1949:62–65; Wormington 1978:46–47).

CORN. Various hypotheses have been advanced to explain the origin of this unique cereal. The present best archaeological evidence from the Tehuacán Valley, Puebla, México, indicates a succession from wild pod corn starting ca. 7200 B.P. (Mangelsdorf, MacNeish, and Galinat 1964:541–543). It is believed that corn diffused from Mesoamerica to the north as a pod corn, with subsequent infusions of genetic traits (Mangelsdorf 1950, 1954, 1974; Mangelsdorf and Smith 1949:213–247; Dick 1965:92–98). The oldest southwestern corn is from Bat Cave (late Cochise Culture dated 5500 B.P.). Both the Hohokam and Basket Maker peoples had corn from their beginnings.

SQUASH. Squash species (*Cucurbita* spp.) are thought to be as ancient as maize, again being derived from the south (Whitaker and Bemis 1975). Squashes were domesticated in Mesoamerica at least 9000 B.P. (Cutler and Whitaker 1961). The earliest domesticated species in the Southwest, *C. pepo,* is known from Cordova and Tularosa Caves and at Bat Cave (5500 B.P.) in the Mogollon region (Martin et al. 1952; Dick 1965). The earliest verifiable remains of *C. mixta* and *C. moschata* in the southwest are from Pueblo II times (A.D. 900–1050), many centuries after the first appearance of *C. pepo.*

BOTTLE GOURD. The one species of bottle gourd, *Lagenaria siceraria,* is common to the Old and New World (Cutler and Whitaker 1961). It appears in the Mexican archaeological record at 9000 B.P. (Tamaulipas, MacNeish 1958). The bottle gourd appears in remains dated at around 2300 B.P. in Tularosa and Cordova Caves in the Mogollon area (Martin et al. 1952:475). Verifiable remains from the Anasazi area are from A.D. 608–683 and 610 (Cutler and Whitaker 1961). The Hohokam had the gourd by the Sacaton Phase (A.D. 900–1100; Haury 1976:183).

BEANS. Two species of beans were particularly important in Southwestern cultures. The oldest known, a kidney bean (one variety of *Phaseolus vulgaris*), appears in deposits dated between 3000 and 2500 B.P. in Bat Cave (Dick 1965:98–99). In Tularosa Cave it appears in remains from 2300 B.P., along with maize and pepo squash (Kaplan 1956:218). The Hohokam had the kidney bean before 2000 B.P. (Haury 1976:118, 346; Bohrer 1970:425), but the Anasazi probably acquired it later in Basket Maker III times (Amsden 1949:132; Wormington 1978:55). It appears in the archaeological record in Tamaulipas and the Tehuacán Valley of México 5000 to 7000 B.P. (Kaplan 1967).

A second bean species important in Southwestern cultures is the tepary (tepari) (*Phaseolus acutifolius*). The tepary appears among the Hohokam remains in the Sacaton Phase of Snaketown (A.D. 900–1100; Haury 1976:118, 338; Kaplan 1956:219) and in deposits near Tucson dating from about A.D. 900–1200 (Bohrer, Cutler, and Sauer 1969:4–5). Carlson (1963) records teparies from a Basket Maker III site dated ca. A.D. 700. The tepary was apparently absent from Bat Cave (Smith 1950; Dick 1965:98–99) and Tularosa and Cordova Caves (Martin et al. 1952:474–475). Kaplan (1956:218) suggests the tepary was introduced to the Mogollon area after A.D. 1100. MacNeish (1964:534) recorded it as a domesticate in the Coxcatlán Phase of the Tehuacán Valley, Puebla, between 7200 and 5400 B.P. (see also Kaplan 1967:208–210).

Two other species of beans, the lima, *Phaseolus lunatus,* and the jack bean, *Canavalia ensiformis,* were grown in the Southwest (Kaplan 1956). The lima appears in late deposits (A.D. 1200–1400 in the Verde Valley, Arizona). *Canavalia,* a tropical derivative, appears in Hohokam, Anasazi, and Salado ruins dated about a century later (Sauer and Kaplan 1969).

COTTON. Cotton, *Gossypium* sp., was a cultivar in the Tehuacán Valley, Puebla, as early as 5400 to 4300 B.P. (MacNeish 1964:536). The Hohokam probably arrived with this crop (Haury 1976:118, 346; Bohrer 1970:425). Some cotton fiber is present in Tularosa Cave (Martin et al. 1952:475). Cotton cloth made its initial appearance here at the beginning of the San Francisco Phase (ca. A.D. 700), as did the bow and arrow. McGregor (1965:246) and Wormington (1978:69–70) place the introduction of cotton to the Anasazi region during Pueblo I period (A.D. 700–900). This cultivar is a Mesoamerican derivative (see Kent 1957 for a discussion of origins).

MACAW. The Scarlet Macaw, *Ara macao,* and the Military Macaw, *A. militaris,* were kept in captivity by early Southwestern peoples. The Scarlet Macaw was an important trade item to all the Southwestern cultures beginning about A.D. 1100 (Hargrave 1970b). Of the two, the more southerly and the more brightly colored Scarlet Macaw accounts for most of the identifiable records. In southern Utah, the northern periphery of Anasazi culture, only macaw feathers have been recovered from archaeological sites (Hargrave 1970b:29; Emslie and Hargrave 1978; Hargrave in press).

Di Peso (1974c:272–273) discusses use and trade in Mesoamerica. In northern Chihuahua, 322 Scarlet Macaw skeletons were recovered from Casas Grandes ruins. The presence of all age stages (including eggs, nestlings, and juvenals) as well as adobe breeding pens indicates that this city was an important breeding center for the late macaw trade to the north (Di Peso 1974b:182–185; Di Peso 1974c:267, 269, 272–273; McKusick 1974). Macaws were a source of feathers for ceremonial purposes. Lifelike macaws, some eating corn, are depicted in late pueblo kiva (ceremonial room) murals (Smith 1952; Hibben 1975). The descendants of the Anasazi still use macaw and other parrot feathers ceremonially.

CULTURAL EXCHANGE BETWEEN MESOAMERICA AND THE SOUTHWEST

The advanced civilizations of México and Central America profoundly modified the southwestern cultures through time. Their influence included not only the exchange of ideas, raw materials, and manufactured items, but also the direct transmission of cultivars (corn, squash, gourds, beans, and cotton) and live birds (macaws). Although this exchange extended over two millenia, dynamic periods of especially strong influence can be detected. Early in the proto-agricultural and early agricultural record there were considerable temporal differences as to when elements were acquired by various recipient cultures (contrast Mogollon with Anasazi, for instance). But by A.D. 700 a definable constellation of derivatives, mostly Mesoamerican, arrived cross-culturally in the Southwest (Table 2). Many of these elements represent genetic modifications of crops from the advanced cultures to the south.

Di Peso (1974a:104) perceives A.D. 700 ± 50 as a period of great transition between Mesoamerica and the northern frontier: "Something occurred which stirred some of the northern frontiersmen. Perhaps it was a motivation which emanated from the great cities located south of the Tropic of Cancer. Here the famed Teotihuacán culture of the Mesa Central had just come to a disastrous end. . . . In the Tehuacán Valley, it was the time of the Venta Salada Phase, when full-time agriculturalists irrigated their fields and lived in large communities associated with separate ceremonial cities. It is thought that in certain areas south of the Tropic of Cancer, the population increased 5000-fold over the original number. Many of these people were engaged not only in agricultural pursuits but in commerce, salt-making, cotton processing, and other industries which raised their living standards."

Di Peso's *Puchteca* (merchant) class may have arisen at this time. For earlier periods, actual routes are less well known. At any rate, in the centuries following A.D. 700, an enormous network in trade in turquoise and other minerals, ceramics, birds, feathers, hides, textiles, shell, and slaves developed between the city of Casas Grandes in Chihuahua and the surrounding northern frontier, extending throughout Hohokam, Mogollon, and Anasazi country (Di Peso 1974b: note especially pp. 129, 144, 171, and 193).

As with the various cultivars, turkeys, a small breed of *M. gallopavo,* were present in the Mogollon area by 2000 B.P. (Tularosa Cave). There were several breeds imported (McKusick this vol.), most likely from several source areas. About A.D. 700, *whole* turkeys, not just feathers, appear in the southern Anasazi archaeological record. Complete turkeys did not arrive in southern Utah until Pueblo II time, around A.D. 900 (Emslie and Hargrave 1978). The turkey spread among agricultural people (except the Hohokam) raising three subsistence crops (corn, squash, and beans). The addition of the third crop (beans) apparently gave a sufficient caloric base for maintaining turkeys as a domestic animal, not generally used as food. Another cultigen (or perhaps only a cultivar), the sunflower (*Helianthus* spp.), may have been an additional source of turkey feed.

From around A.D. 1350 to 1450, the entire Southwest underwent a period of population decline and areal contraction known to archaeologists as "The Great Abandonment." Although the decline was most conspicuous in the Anasazi on the Colorado Plateau because of the great number of large masonry sites, the Hohokam also disappeared at this time, and the Mogollon/Mimbres Culture a little earlier (Haury 1976:351–357; Wormington 1978:107, 144, 161, 166; McGregor 1965:420–421, 426, 428, 433). Thus, the demographic sequence consisted of a slow (±1000 years) population buildup and expansion, followed by a rapid decline. Though intensively studied and debated by archaeologists, ecologists, dendroclimatologists, geologists, and palynologists, no simplistic solutions satisfactorily explain the causality of the Great Abandonment. Perhaps the combined demographic/ecologic model of Martin and Plog (1974:318–333) comes closest.

Regardless of causal factors, the results were the same: Pueblo and puebloid-influenced population centers almost completely disappeared. These included the villages with their great herds of turkeys (McKusick this vol.). Flocks were abandoned to fend for themselves. I propose that at this time, if not before, the turkey became feral locally throughout what is the modern range of the subspecies *M. g. merriami* (Fig. 1). It filled the niche in suitable habitats left vacant by the Pleistocene *M. crassipes* north of the range of the Sierra Madre

Occidental subspecies, *M. g. mexicana. Meleagris g. mexicana* probably occurred as far north as the border ranges of southwest New Mexico and southeast Arizona, below the Mogollon Rim (Aldrich and Duvall 1955; Phillips et al. 1964). Such a distributional pattern is shared by a number of other essentially Mexican montane or encinal vertebrates, including *Crotalus lepidus, C. pricei, C. willardi, Otus trichopsis, Peucedramus taeniatus, Junco phaeonotus, Nasua narica,* and *Mephitis macroura.* Native *M. g. mexicana* has been extirpated from these border ranges (Chiricahuas, Huachucas, Baboquívaris, Santa Catalinas, Santa Ritas, Peloncillos, and probably the San Luis Mountains). Some of these areas have been restocked with *M. g. merriami.* Only a few specimens of *M. g. mexicanus* were collected and preserved prior to this restocking, and these records suggest the former northern limit of the Sierra Madrean subspecies.

MELEAGRIS GALLOPAVO MERRIAMI: A FERAL POPULATION?

The presumption has been that the turkey, *M. g. merriami,* occurred wild throughout suitable parts of the Southwest and that it was taken captive by the Basket Maker peoples and eventually domesticated. I suggest exactly the reverse of the above assumption. First, that Mesoamerican turkey feathers were brought to the Anasazi area by trade. Next, the live bird was imported as a domesticate, and later it became feral throughout the range of *M. g. merriami.* S. Emslie, C. McKusick, and B. Wright are of the opinion that turkeys escaped from domestication quite early, long before the Great Abandonment. The details of when the various domestic breeds and the wild form appear in the different cultural areas are discussed by McKusick (this vol.).

Some areas of the Southwest—parts of Utah, and the North Kaibab Plateau and the Hualapai Mountains of Arizona—lack native populations of *M. g. merriami* yet have suitable conifer or pine-oak habitat to support turkeys. Some of these areas (Fig. 3) have been successfully stocked in recent decades (Schorger 1966:438–439, 459). The historical absence of turkeys in these ranges tends to support the feral turkey hypothesis. *M. g. merriami* historically occurred in habitats where aboriginal peoples carried on a turkey industry or in immediately contiguous pine-oak habitats. Parmalee (this vol.) found no turkey bones among the numerous Galliformes recovered from 16 archaeological sites (5 Archaic and 11 Fremont) in Utah. Sinaguan, Patayan, Virgin River Anasazi, and Fremont peoples were not turkey raisers (McKusick this vol.). The disjunct forests in these cultural areas historically lacked turkeys. But other, similarly discontinuous habitats within the turkey-raising Anasazi area (e.g., the Lukachukai and Chuska Mountains) did host native populations.

A number of plants have become locally feral, self-maintaining populations in the arid West, after the abandonment of Anglo-European mining or ranching sites: various mustards, *Brassica* spp.; horehound, *Marrubium vulgare*; iris, *Iris* sp.; tree of heaven, *Ailanthus altissima*; to mention a few. Some southerners brought the opossum, *Didelphis v. virginianus,* to California early in the twentieth century and it rapidly spread throughout suitable parts of the state (Grinnell, Dixon, and Linsdale 1937). The Old World honey bee, *Apis mellifera,* is now widespread in the feral state. The escaped burro, *Equus asinus,* maintains stable populations on the Lower Colorado River drainage, partially filling a niche vacated by several Pleistocene species of horses, *Equus* spp. These examples demonstrate how easily feral populations may be established.

VARIATION IN EARLY CULTURAL TURKEYS

The early *M. gallopavo* that appeared in the Southwest were hardly uniform in characters. Schorger (1961) reported a relatively small mummified adult male turkey from Tularosa Cave, implying that it was a captive bird. Its distinguishing characteristic was a neck feathered to the base of the skull. Later Schorger (1970) formally described this anomaly as *M. g. tularosa,* based on two specimens from different localities. The original site description (Hough 1914:5–6) leaves little doubt that it was a domestic form: "A desiccated adult bird, parts of other individuals, desiccated chicks, and a number of eggs were found in a portion of the cave which was evidently a pen where turkeys were kept in captivity, there being great quantities of the droppings of the birds in the debris." McKusick (this vol.) finds two basic size varieties in prehistoric sites from the Southwest. Her Small Indian Domestic is the same as Schorger's (1970) *M. g. tularosa* "subspecies," and her Large Indian Domestic corresponds to present-day wild *M. g. merriami.*

Hargrave (1970a) examined feathers of a small brown-toned turkey in Sand Dune Cave (Basket Maker II, A.D. 700 or earlier), and gave these the formal name *M. g. coltoni.* All the feathers appeared to be from a single individual. According to McKusick (pers. comm.) these are juvenal-plumaged. Since normal black and white feathers occurred in the site, Hargrave reasoned that his new "subspecies" was not the result of postmortem color changes ("foxing"). Emslie and Hargrave (1978) reported additional "*M. g. coltoni*" feathers from Westwater Ruin, San Juan Co., southeastern Utah (Basket Maker III/Pueblo I, ca. A.D. 700). I do not advocate formal nomenclatural recognition of the individual strains "*coltoni*" and "*tularosa*" because they were undoubtedly domestic birds.

CHARACTERISTICS OF THE SUBSPECIES OF COMMON TURKEY

If the turkeys that now make up the subspecies *M. g. merriami* did not evolve locally, then what was their source? There are two possibilities: from the east or from the south. The eastern woodland cultures had a subsistence base of maize, squash, and beans, but did not domesticate the turkey; they hunted it in the wild (Schorger 1966:137). In the eastern part of the United States the turkey has a long continuous fossil record, extending back to the Miocene (Steadman this vol.). The eastern races (*M. g. sylvestris, M. g. intermedia,* and *M. g. osceola*) do not have subspecific characters that would suggest that *M. g. merriami* was derived from them (Table 2). The eastern races are strongly refuscent, intermediate to small in size, and lack the whitish-tipped lower rump. The races to the south appear to me to be better candidates. *M. g. merriami* may have been derived from the Large Indian Domestic breed, and this, in turn, from *M. g. gallopavo* and/or *M. g. mexicana.* The southernmost *M. g. gallopavo* is colored almost like *M. g. merriami* on the rump, tail coverts, and the tips of the rectrix, but it is considerably smaller. *M. g. mexicana,* which ranges geographically between *M. g. gallopavo* and *M. g. merriami,* is the same size as *M. g. merriami*. The bimodal size variation within each sex of puebloid turkeys (McKusick this vol.) suggests at least two parental stocks. Schorger's observation (1970:170) that his "*M. g. tularosa*" had little white in the wings and no apparent white in the rump suggest a non-Mexican source for the Small Indian Domestic breed. Its coloring, as well as its small size and odd neck feathering, do not match any wild population living today. Modern *M. g. merriami* is apparently homogeneous throughout its extensive range, with no evidence of "*M. g. tularosa*" influence. With at least five centuries of selection in the wild, loss of the great variability would be expected. McKusick (pers. comm.) believes it is futile to speculate on the origin of races since the Common Turkey has been domesticated and transported in Mesoamerica for over 4000 years.

Little is known of archaeological turkey distribution and domestication in México. Flannery (1967) found turkey in remains from about A.D. 180 (Palo Blanco phase) in the Tehuacán Valley. This is *south* of the range of wild *M. gallopavo,* in habitat that was then, as now, highly xeric (cactus-thornscrub desert). Both the domestic turkey and the dog were eaten with increasing frequency in the Tehuacán area until the time of conquest. In the Valley of Oaxaca, Flannery (pers. comm. to Hargrave) found that domestic *M. gallopavo* appeared around 2400 B.P. These are still farther from the wild range. Apparently agricultural peoples took this domesticate both to the north and to the south. Archaeological turkey remains dating A.D. 700–1300 have been found on the coastal lowlands of northwestern México, below the known range of *M. gallopavo* (Stuart Scott and Elizabeth Wing pers. comm.). This is further evidence for importation and domestication.

CONCLUSIONS

Two hypotheses are suggested by the present osteological data. The first is that only *M. crassipes* was present in the Southwest (north of the Sierra Madrean outliers) during the late Pleistocene and the early Holocene. The available data thus far support this idea. No fossil *M. gallopavo* are known from within the modern range of *M. g. merriami. Meleagris crassipes* and *M. gallopavo* have not been found together. Nor has *M. crassipes* been found associated with proto-agricultural or agricultural peoples (Archaic stage or later).

The second hypothesis is that at least two stocks of *M. gallopavo* were imported into the Southwest from the south, the east, or both, by peoples with a multi-crop subsistence base after the extinction of *M. crassipes*. The spread of *M. gallopavo* appears to be directional, following the diffusion of Mesoamerican cultigens. Turkeys from late Archaic deposits in southern New Mexico are undated. The oldest dated turkeys are from the Mogollon cultural area. Trade in turkey feathers preceded the trade in whole birds. After several centuries turkeys appeared in the southern Anasazi area, then in the northern Anasazi regions. Peripheral cultural areas to the west have little or no evidence of turkey. Although the Fremont culture had corn agriculture and apparently suitable habitat for turkey, the bird itself was probably not taken that far north. However, lacking any barriers, feral turkeys may have spread from the Mesa Verde area of southwestern Colorado throughout much of that state, resulting in the present range of *M. gallopavo*.

A third hypothesis, that domestic strains of *M. gallopavo* preceded the wild form, *M. g. merriami,* in each cultural area, is a part of McKusick's study (this vol.). The idea of the importation of Common Turkey stocks by Indians comes from Hargrave (1970) as well as Schorger (1961, 1966, 1970).

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Many people contributed ideas that became incorporated into this study. Credit must first go to the late ethnobiologist, Lyndon Lane Hargrave, who suggested a critical look at fossil turkeys. Storrs Olson and David Steadman both turned over to me their data on *M. crassipes* from a number of southwestern sites, and Steadman assisted with many of the identifications. Charmion McKusick assisted with the cultural aspects from her years of study of this species in archaeological contexts. Both Steadman and McKusick offered extensive comments on earlier drafts of this paper. Steve Emslie and Barton Wright read the paper and shared their expertise in southwestern archaeology.

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THREE GROUPS OF TURKEYS FROM SOUTHWESTERN ARCHAEOLOGICAL SITES

By Charmion R. McKusick[1]

ABSTRACT: The study of a minimum of 6713 whole or partial turkey skeletons from 95 southwestern archaeological sites dating between ca. 300 B.C. and A.D. 1723 has resulted in the differentiation of three groups of turkeys that are separable from each other and from all other turkeys known to have occurred in the Southwest:

(1) The Small Indian Domestic, *Meleagris gallopavo tularosa,* first appeared between ca. 300 and 150 B.C. in the Mogollon Culture Area of west central New Mexico coincidentally with the establishment of a stable agricultural food supply, peaked in the Eastern Periphery Pueblos, and became extinct with the fall of the Pueblos in 1672.

(2) The Large Indian Domestic, *Meleagris gallopavo merriami,* appeared in the Anasazi Culture Area in northeastern Arizona about A.D. 400 along with the beginnings of agriculture. The Large Indian Domestic is the predominant race of turkey in southwestern archaeological collections dating from its first appearance about 400 A.D. until 1723, the last known date for large flocks of Indian turkeys.

(3) Merriam's Wild Turkey, also *Meleagris gallopavo merriami,* may have been present as a feral form of the Large Indian Domestic as early as A.D. 500, and feral turkeys clearly identifiable as Merriam's Wild Turkey existed shortly before A.D. 600.

The study of turkeys from southwestern archaeological sites summarized herein was undertaken as the result of the discovery in 1967 that the remains of over 900 turkeys recovered from the excavation of Mound 7, Gran Quivira National Monument, New Mexico, were unlike any previously studied from southwestern archaeological sites. This unusually homogeneous group of small, gracile-boned turkeys with humped backs and short tarsi raised the question of the time and place of their domestication, and the identity of the wild progenitors of southwestern Indian turkeys in general. As is often the case when several investigators are working on the same problem without each other's knowledge, they tend to arrive at the same conclusion simultaneously, but from different directions. The late A.W. Schorger, an outstanding authority on the wild turkey, wrote to T.W. Mathews of the Southwest Archaeological Center, Globe, Arizona, in the summer of 1969 seeking information relative to a desiccated short-shanked turkey with a fully-feathered neck from a southwestern archaeological site that he was studying. Mathews supplied him with the series of measurements I had taken from the Mound 7 turkeys. From a comparison of characters and measurements it became obvious to all three of us that the Tularosa mummy was a specimen of the small breed known only from skeletal elements at Gran Quivira. Based on our combined data, Schorger (1970:168–170) described the Tularosa Turkey as a new extinct subspecies, *Meleagris gallopavo tularosa,* in January of 1970.

Although Schorger's enquiry resulted in a concerted effort to solve the turkey problem, the problem itself had been around a long time. I had discussed the Indian domestic turkeys, their origin and development with the late Lyndon L. Hargrave, Erik Reed, and Mathews in 1963, but no plan of research was proposed. The subject came up again when Alden C. Hayes submitted his avian collection from the excavation of Mound 7 at Gran Quivira National Monument for identification. To complete this study, I found it necessary to isolate diagnostic characters of the three groups of Indian turkeys. Mathews confirmed the validity of these characters in producing reliable identifications. A.W. Schorger reviewed the entire project before his death, and wrote to us that our findings agreed with his. Small Indian Domestic Turkeys, Large Indian Domestic Turkeys, and Merriam's Wild Turkeys may be distinguished from each other by comparison of characters of the mandible, pelvis, coracoid, scapula, humerus, carpometacarpus, femur, and tibiotarsus, as well as by means of measurements of sample populations. Illustrations of the age stages of the three groups of turkeys (which are pertinent to the archaeologist's reconstruction of the yearly round of human activity), the diagnostic osteological characters of the three groups, and the means of measurements of the sample populations are found elsewhere (McKusick 1980).

The capability of segregating the various groups of turkeys that occur at prehistoric habitational sites in the Southwest made it possible for the first time to test the various hypotheses of turkey origins and distribution.

1. Reed (1951), citing Hargrave's observation that turkey pens are found in areas where wild turkeys do not now exist and where there is no evidence of there ever having been any, hypothesized that turkeys were hunted in areas where they were available as wild birds and were raised in areas where they were not.
2. Reed (1951) further hypothesized that turkeys were eaten mostly by the northern Anasazi and their cultural descendents.
3. Johnson (1965) hypothesized that hunting turkeys rather

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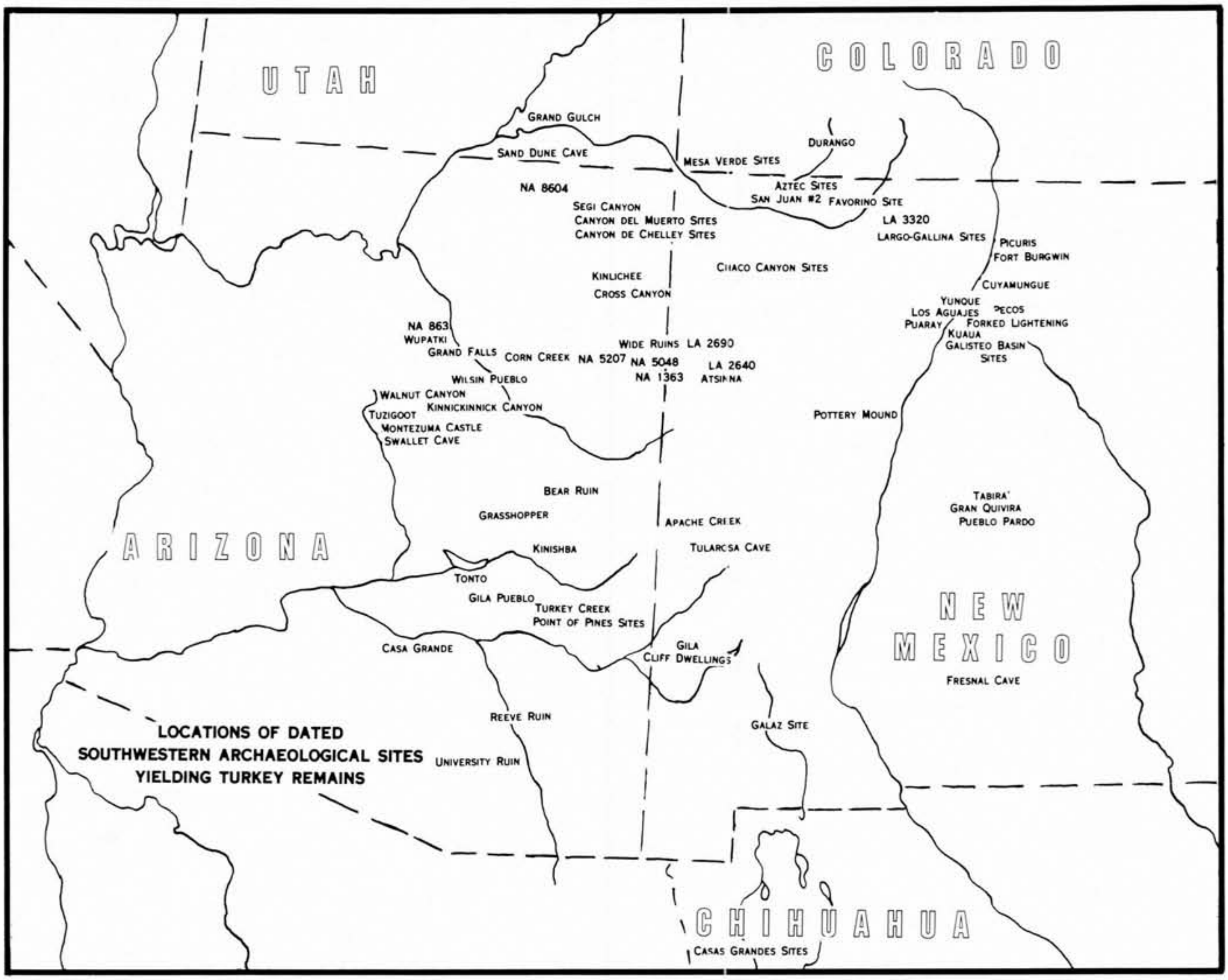

Figure 1. Locations of dated southwestern archaeological sites yielding turkey remains.

than raising them was a diagnostic trait of Western Pueblo Culture.

4. Hargrave hypothesized (pers. comm. 1963) that aberrant turkey bones recovered from southwestern human habitational sites represented remnants of Pleistocene forms. He did not attempt to explain how the Indians had obtained these forms, or why they had supposedly persisted into the fourteenth century A.D.

5. Hargrave discussed (pers. comm. 1963), and Rea (this vol.) tested, the hypothesis that modern Merriam's Wild Turkeys are descendents of feral domestic turkeys, rather than that Indian domestic turkeys are the descendents of indigenous wild forms.

6. McKusick hypothesized in 1968 (Western Archaeological Center Avian Files) that Indian domestic turkeys were introduced into the Southwest as part of the Formative Level Cultural Complex or Complexes (corn, beans, squash, permanent housing, pottery, social stratification) from some place or places outside the Southwest.

Recently, A.M. Rea's interest in *Meleagris crassipes* re-opened the issue of the southwestern specimens identified as Pleistocene and pre-agricultural turkeys. This project made it necessary for me to re-examine all turkey bones from southwestern archaeological human habitational sites that had been set aside as Pleistocene remnants, just as Rea was re-examining all pre-Formative Stage specimens that had been formerly identified as *M. gallopavo*. Rea did not provide me with a hypothesis to test in this project, rather he asked for a review of the specimens and an objective evaluation of their identification.

METHODS

In this study, variables such as age stages and sexual dimorphism were determined before subspecific differences or differences between wild and domestic forms of the same subspecies were considered. I raised poults of the modern table breed, *Meleagris gallopavo gallopavo,* to adulthood to secure data on differential rates of growth of males and females through their developmental stages. I obtained skeletons to represent the desired osteological age classes from free-ranging domestic turkeys. In addition, C.A. Thomas of the Southwest Archaeological Center enlisted the aid of Gila County, Arizona, turkey hunters. I examined turkeys from both spring and fall hunting seasons, collecting head, feet, and feather samples, noting the color of vane, rachis, and legs, recording the sex, and tagging the carcass for matching of the bones and samples after the birds were roasted and eaten. Seven age stages were defined to answer specific questions for the archaeologist about aboriginal turkey usage, turkey culture, and the yearly round of human activity (McKusick 1979).

Information on age stages and sexual dimorphism also proved useful in the proper identification of a series of specimens that Hargrave had accumulated at the Southwest Archaeological Center, Globe, Arizona, from collections studied between the early 1930's and 1968. These had been referred to Pleistocene forms in spite of the fact that they were found in collections from human habitational sites in the Southwest, some of which have been dated as late as A.D. 1340.

Data on the Small Indian Domestic Turkey, *Meleagris gallopavo tularosa,* are based on an unmixed population of 923 individuals from Mound 7, Gran Quivira National Monument, New Mexico. Data for the Large Indian Domestic Turkey, *Meleagris gallopavo merriami,* are based on an early, unmixed, classic population of 32 individuals from Tse-ta'a, Canyon de Chelley, Arizona. Archaeological samples of Merriam's Wild Turkey, also *Meleagris gallopavo merriami,* are too fragmentary to be useful in establishing ranges of measurements; therefore, modern wild specimens were employed.

As the study progressed, it seemed advisable to test methods and criteria against as many collections from as many areas of the Southwest and as many time periods as possible. Accordingly, every turkey specimen available for loan from southwestern archaeological sites was borrowed, examined, and where possible, measured.

SOUTHWESTERN TURKEYS IN TIME AND SPACE

I derived the time data and geographical locations found in this section from file records and publications of the institutions that loaned the specimens I examined, and from personal communication with individuals who performed or were familiar with the excavations of the sites from which the specimens were recovered. Site locations are indicated on Fig. 1.

For the purpose of easy comparison, I shall discuss the sites by the time periods established by Willey (1966:188) for cultural designations of the Anasazi Culture, since in no other cultural area did turkeys assume such an important role in the economy and life of the people. It is recognized that the populations of some areas, such as Chaco Canyon, reached a given cultural level earlier than the main stream of Anasazi development, while others, such as the western Basket Maker, lagged considerably. To the non-archaeologist reader, cultural development at some sites may seem slightly out of phase with the main stream of southwestern development, but this is a well-recognized phenomenon that in our modern day culture is illustrated by the contrast between the cultural manifestation in Manhattan, a medium-sized midwestern town, and a backwoods farm in Appalachia. What is important in this study is the date of occurrence of the turkeys, their breeds, and their relationships to the inhabitants of the site at which they were found.

PROTO-AGRICULTURAL AND BASKET MAKER II

300 B.C. to A.D. 400, Fig. 2

The only occurrence of turkey feathers in the Southwest that has been referred to a Proto-Agricultural context is that reported from the excavation of Fresnal Cave, LA10101, near Cloudcroft, New Mexico, which dates from ca. 2500 B.C. to ca. A.D. 1 (Vorsila Bohrer pers. comm.). Turkey feathers from this cave are mainly the irridescent tips of body feathers; only a few specimens are from wing coverts or the tail. The collection includes rachis sections stripped of their vanes in a manner associated elsewhere with the production of feather cordage. Therefore, I believe these turkey specimens represent a level of cultural development no earlier than Basket Maker II, and I have included them here despite the greater antiquity of the major portion of the collection.

In undisputed Basket Maker II levels, turkey feather blankets occur in addition to rabbit fur blankets in such areas as Grand Gulch, Utah; Durango, Colorado; and Canyon del Muerto, Arizona (Morris 1939:18). Excavations at Canyon del Muerto have also produced from a Basket Maker II level the headless mummy of a Small Indian Domestic (a "Tularosa Turkey") with vegetal cordage around its neck. It was dated at ca. A.D. 250 on the basis of associated cultural material by R.G. Vivian (Southwest Archaeological Center Photo Files). R. Richert, who is familiar with the circumstances of the find, believes this is a conservative date; i.e., the bird may be even older (Richert pers. comm.).

Bones of four Small Indian Domestics from Tularosa Cave, New Mexico, occur in Pre-Pottery Phase levels dated by Martin et al. (1952:483) at ca. 300 B.C. ± 150–200 years.

The more western Basket Maker II peoples of the Kayenta area of northeastern Arizona apparently were behind their eastern counterparts in the use of turkeys, since Guernsey and Kidder (1921:111) did not find any feather-string in these sites. I re-examined the feather collection from Woodchuck Cave, a Basket Maker II burial cave dated at A.D. 200 ± 100 years (Locket and Hargrave 1953). There are two specimens of passerine feather cordage, one a Z-twisted skin strip and the other a skin strip with feathers Z-wrapped on a two-ply Z-twist vegetal core, but only one specimen of whole-feather turkey wrapping (Specimen No. 3112/B6.30). No turkey bones were recovered from this cave, and turkey feathers are so few that it is probable that they were trade items, since wild turkeys are not known from this area at any time level. Du Pont Cave in Utah, dated by tree rings at A.D. 217 (Lockett and Hargrave 1953:31), contained no turkey cordage, only the type of cordage wrapped with strips of skin of small birds (Nusbaum et al. 1922:104).

Evidence of cultural lag is found at Sand Dune Cave near Navajo Mountain, Utah, where the Basket Maker II period is dated A.D. 300 to A.D. 700 (Hargrave 1970). Here are found only bundled turkey feathers, and no feather cordage even in a time period that was elsewhere Basket Maker III. In this case, far beyond the known range of wild turkeys, feathers are presumably those of domestic birds traded in from another area, probably Canyon de Chelley or Canyon del Muerto, Arizona.

BASKET MAKER III

A.D. 400–700, Fig. 3

Both at Mesa Verde, Colorado, and at Tse-ta'a in Canyon de Chelley, Arizona, the Large Indian Domestic Breed was predominant. Skeletal remains from this period show no indications of food use, and presumably the birds were used only for their feathers. Morris (1941:197, 201, 202) reported turkey pens between the Basket Maker III slab and pole houses ex-

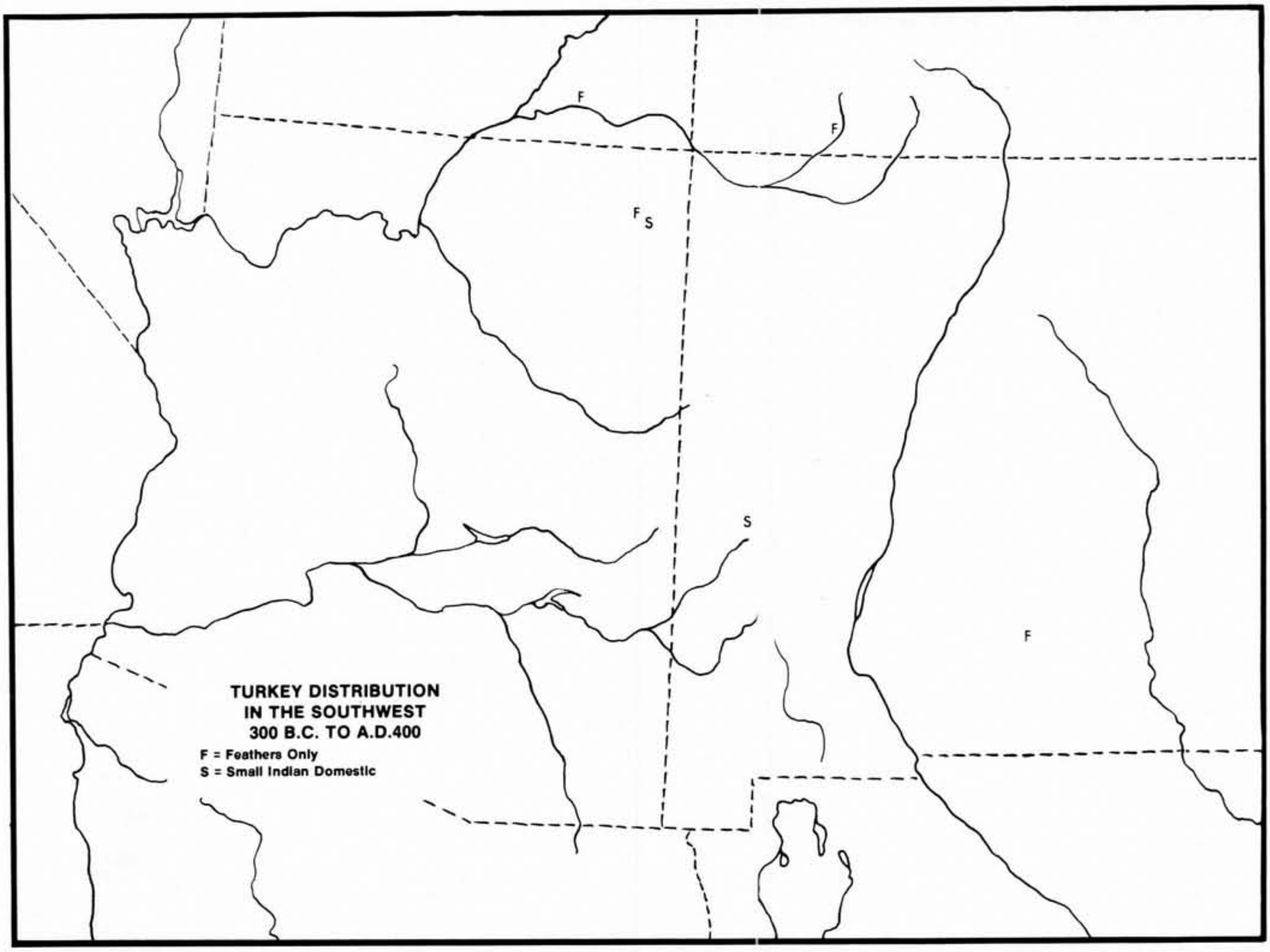

Figure 2. Turkey distribution in the Southwest from 300 B.C. to A.D. 400.

cavated at Tseahatso and the surrounding cave wall. Approximately 300 (Lee Abel pers. comm.) natural mummies of turkeys that had apparently died of old age were excavated from this cave. In addition, one young turkey that had suffered a broken leg was found. The injured limb had been set, bound with soft fiber, and splinted. In spite of this careful attention, the bird died and was buried with the splints still in place.

W.D. Lipe excavated the bones of Large Indian Domestic Turkeys from Site GG70-187, about 3 km east of Grand Gulch, Utah, associated with Basket Maker III cultural materials that probably date into the A.D. 600's. These are classic specimens that compare well with those from Tse-ta'a in Arizona.

Bones of Merriam's Wild Turkey were found at AZ P:16:1, Bear Ruin, in east central Arizona, with remains that date from the seventh century A.D. Two tubes cut from the tarsometatarsi of males, including the spur cores (Haury 1940:14, 116), represent specimens of extremely early worked turkey bone.

In the Point of Pines area of Arizona, a turkey bone was recovered from an early Circle Prairie Phase pit house that probably dates before A.D. 600 (Wheat 1954:179). I have referred it to Merriam's Wild Turkey.

PUEBLO I

A.D. 700–900, Fig. 4

Information on Pueblo I turkeys is scanty. The only material examined is from Site 1205, Site 1678, and Badger House, all on Mesa Verde, Colorado; Tse-ta'a in Canyon de Chelley, Arizona; La 3427, the Favorino Site on the San Juan River, New Mexico; and La 3320, southwest of Dulce, New Mexico. Only the Large Indian Domestic Breed is represented. There is no reliable evidence of the use of turkeys other than for feathers in this period.

Guernsey (1931:92–93) reported finding feather cord robes in Pueblo I burials at Cave 1, Segi Canyon, in northeastern Arizona. Because fur cord robes were included in the same burials, it is probable that the feather cord examples were items of trade and that live turkeys were not yet known in the area.

PUEBLO II

A.D. 900–1100, Fig. 5

During Pueblo II time the Large Indian Domestic Breed spread from its Four Corners homeland as far west as NA

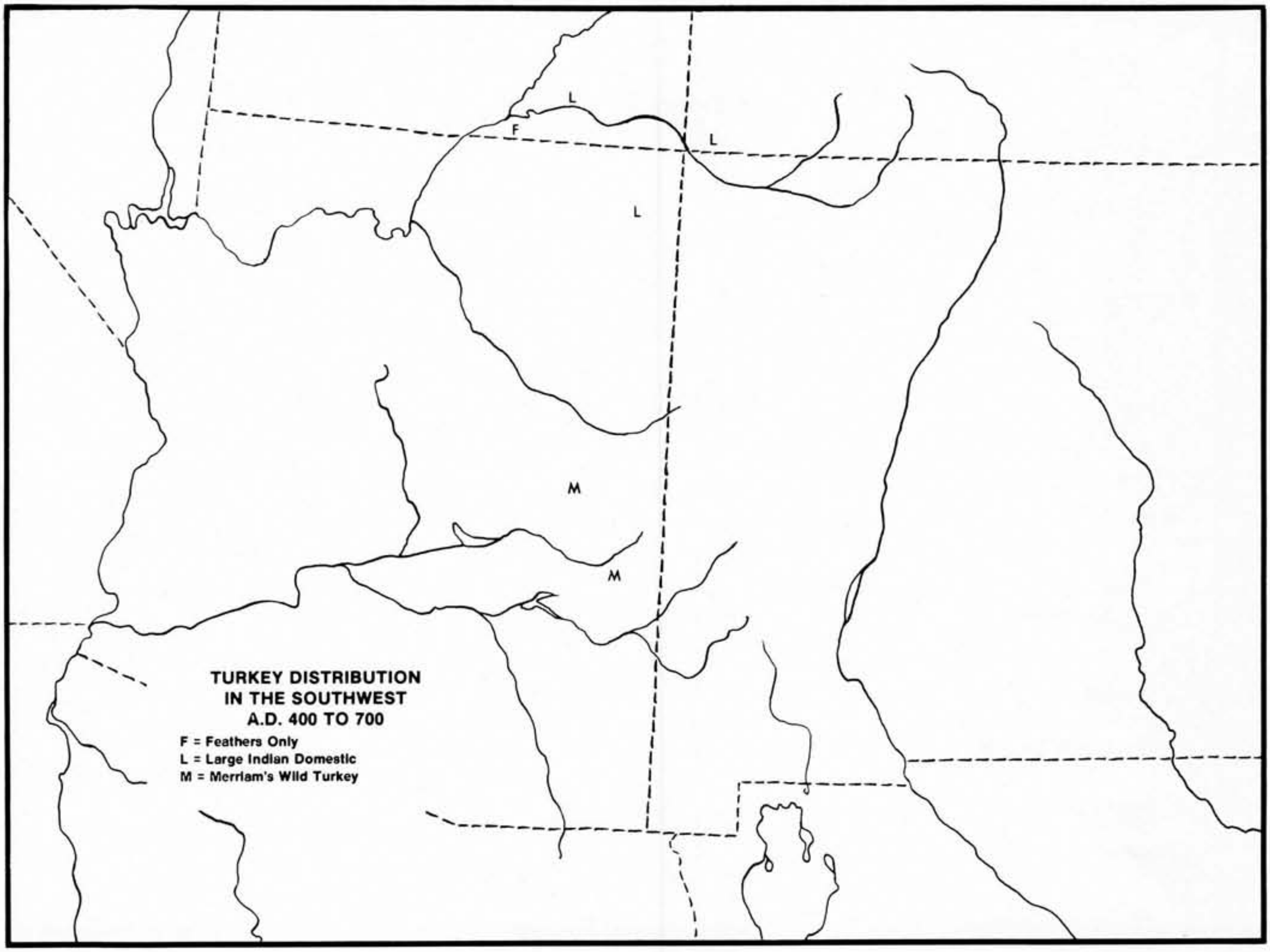

Figure 3. Turkey distribution in the Southwest from A.D. 400 to 700.

8604 near Kiet Siel, Arizona, east to TA 32 near Ranchos de Taos, New Mexico, and south to Casas Grandes, Chihuahua, Mexico, forming a T-shaped distribution.

In contrast to earlier levels that lacked turkey remains, Pueblo II and later levels at Tseh-So in Chaco Canyon, New Mexico, contained many turkey bones (Brand et al. 1937:101, 106). Burials of headless female turkeys were also found in the kivas at this site.

Tularosa Cave, although now included in the area where Large Indian Domestics were predominant, still yielded a feathered mummy of the Tularosa Turkey, or Small Indian Domestic. The occurrence of a Small Indian Domestic at this site may have cultural significance. Four desiccated poults of erythristic coloration and a specimen of bone from Merriam's Wild Turkey were also recovered from Tularosa Cave at levels dated at A.D. 1100 (P.S. Martin pers. comm.).

The one piece of stripped-vane cordage recovered from NA 863, Medicine Cave, in the area of Flagstaff, Arizona, may have been a trade item (Bartlet 1934:46); however, a turkey bone has also been found at a nearby site at the Grand Falls of the Little Colorado. I have referred the latter to the Large Indian Domestic Breed. These occurrences in the Sinagua Cultural Area are out of the main region of turkey raising, and turkeys never assumed any real importance.

Pueblo III

A.D. 1100–1300, Fig. 6

By Pueblo III times the Large Indian Domestic was generally known throughout the Southwest except in the Sinagua and Hohokam Culture Areas of Arizona. The Sinagua peoples had domestic turkeys available, but did not include turkey raising in their cultural complex. Turkey remains found in Sinagua sites were probably traded in from the north and east. The Hohokam peoples appear to have been even more disinterested, as no turkey specimens have been found in Hohokam sites except for two or three specimens from Salado cultural deposits, such as those at Casa Grande, Arizona.

The butchered and broken condition of Merriam's Wild Turkey bones recovered from sites along the Mogollon Rim during this time period indicates that wild turkeys were hunted to a limited extent along this upland area from the Galaz Site in southwestern New Mexico to Walnut Canyon in northern Arizona.

The Small Indian Domestic appeared at Gran Quivira as a homogeneous, well-standardized breed about A.D. 1275. It has been found in much smaller numbers in Pueblo III deposits at Mesa Verde, Colorado, and at Casas Grandes, Chihuahua, México.

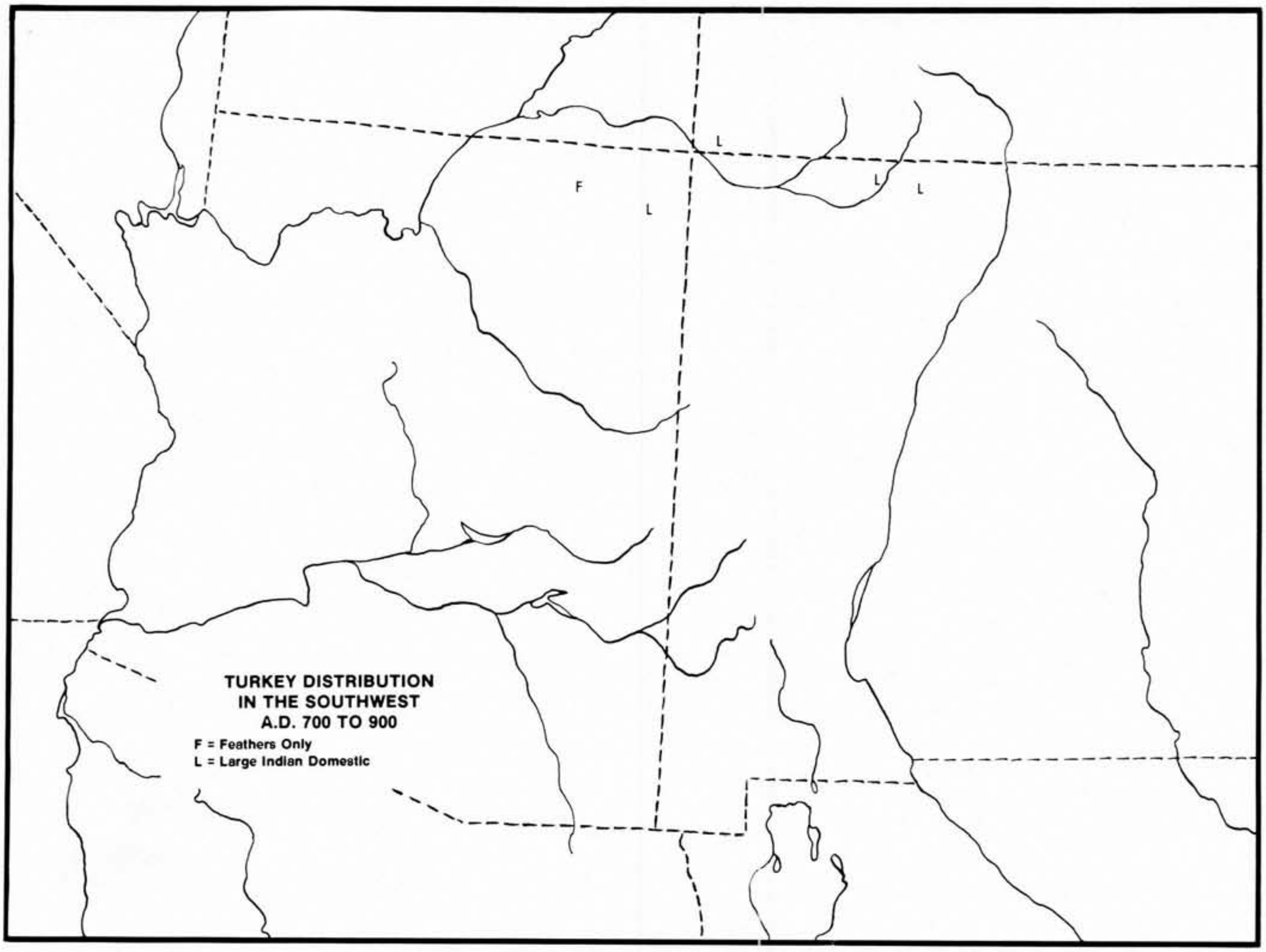

Figure 4. Turkey distribution in the Southwest from A.D. 700 to 900.

PUEBLO IV

A.D. 1300–1700, Fig. 7

The large settlements in the Mesa Verde, Colorado; Canyon de Chelley, Arizona; and Chaco Canyon, New Mexico, areas were vacant by the Pueblo IV period. The center of turkey raising had moved south and east to the Rio Grande and the Eastern Periphery of the Southwest Cultural Area. Although the Large Indian Domestic was predominant, wild turkeys were hunted in the Point of Pines area and at Grasshopper in Arizona. The two specimens from the Verde Valley, Arizona, are also probably Merriam's Wild Turkey, which had been present just to the east as a feral form of the Large Indian Domestic since before A.D. 600.

The Small Indian Domestic Breed reached its peak at this time in central New Mexico at the Tompiro Pueblos of Gran Quivira, Pueblo Pardo, and Tabirá. It was still present at Casas Grandes, Chihuahua, México, in small numbers, along with the much more numerous Large Indian Domestics, until the fall of the city ca. A.D. 1340. Single specimens of the Small Indian Domestic have been found at the University Ruin and Reeve Ruin in Arizona (which date to ca. A.D. 1350), but turkey raising never assumed any importance in this area. An immature specimen from Casa Grande, Arizona, is definitely from a domesticated turkey but is too young to assign to breed. A turkey specimen from Gila Pueblo, Arizona, is so young that it cannot be assigned to breed, wild or domestic.

DISCUSSION OF HYPOTHESES

1. Reed's hypothesis that turkeys were hunted where they were available wild, and raised in areas where they were not.

Reed's discussion (1951) indicated that his thinking centers on the obvious evidence of domestication in the Anasazi Cultural Area. Certainly domestic turkeys were present in the Anasazi Area, but data indicate that they were not domesticated there, but were brought in as a well-established domestic breed from elsewhere.

However, Small Indian Domestics were known in the Mogollon Cultural Area about 500 years before they were known in the Anasazi Area, and about 700 years before the favored Anasazi breed, the Large Indian Domestic, appeared in that area.

Turkeys were hunted along the Mogollon Rim, but not early (indeed, there were none to hunt) or in any great numbers. A few were hunted by about A.D. 600 after the Large Indian

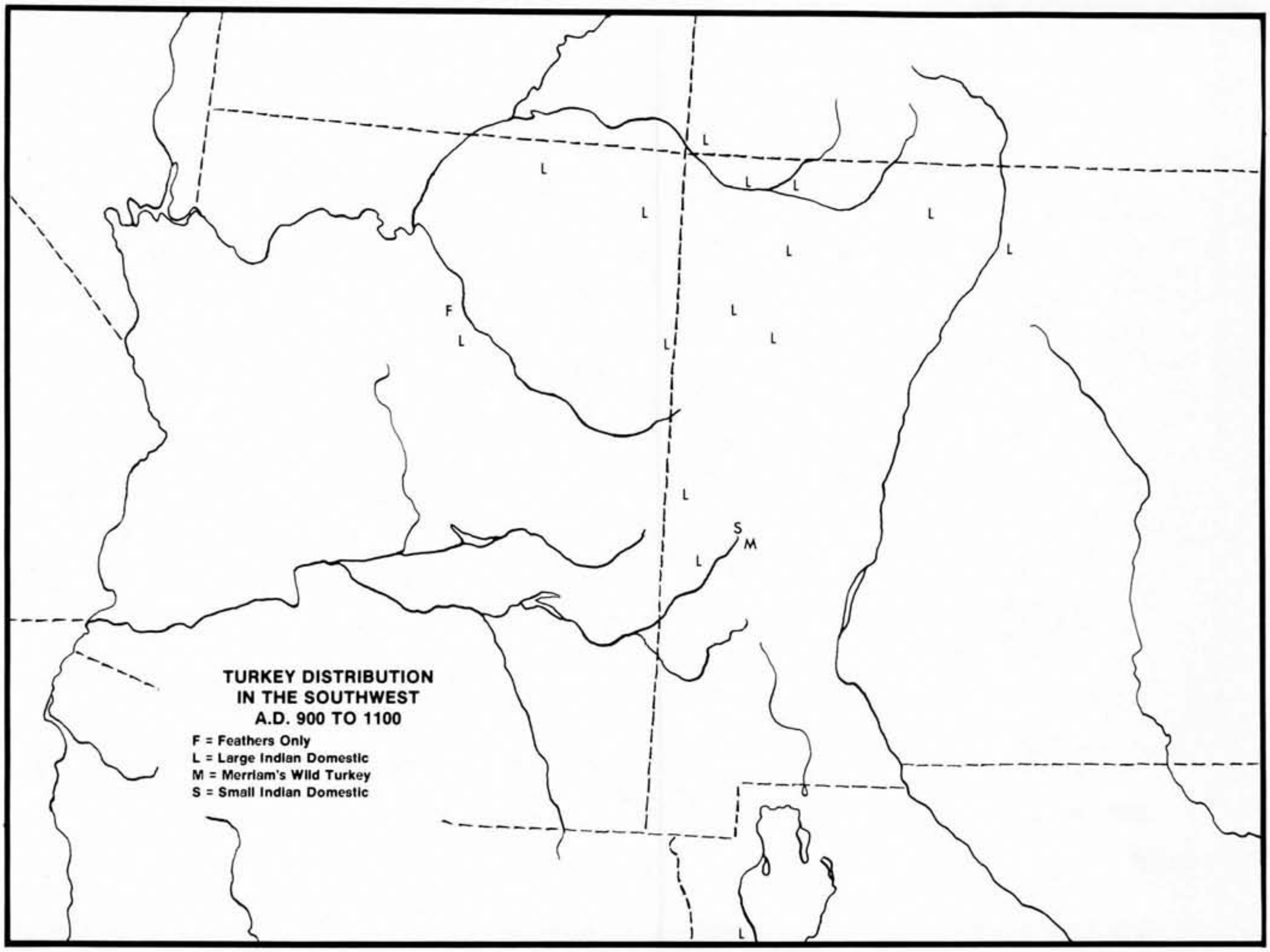

Figure 5. Turkey distribution in the Southwest from A.D. 900 to 1100.

Domestics were introduced and had an opportunity to become feral. More were hunted during the 1200's and 1300's than at any other period, but their remains never approached the number of those of domestics at the excavations in which they were found.

2. Reed's hypothesis (1951) that turkeys were eaten mostly by the northern Anasazi and their cultural descendents.

This is generally true for the Large Indian Domestic Breed. It is interesting to note that no Small Indian Domestics turn up as food refuse anywhere in the Southwest, with the possible exception of one sample at Antelope House, Canyon del Muerto, Arizona. Greatest food use of turkeys occurs on the Mesa Verde, Colorado, and at some of the Rio Grande Pueblos in New Mexico, and involves only Large Indian Domestics. Minor food use of Merriam's Wild Turkeys occurred late, in the 1200's and 1300's, and only along the Mogollon Rim of Arizona and New Mexico.

3. Johnson's hypothesis (1965) that hunting turkeys rather than raising them was a diagnostic trait of Western Pueblo Culture.

Of 17 Western Pueblo avian collections examined, domestic turkeys were present in 16 and wild turkeys in only 6. Thus, turkey hunting does not appear to be diagnostic for Western Pueblo Culture, and is probably a function of geographical location.

4. Hargrave's hypothesis (1963) that Pleistocene forms were present in southwestern archaeological sites.

I have discarded this hypothesis in light of present evidence. The specimens he set aside as not conforming to the general population of turkeys from archaeological sites have subsequently proved to be either immature forms of the Large Indian Domestic, or adults of the Small Indian Domestic.

5. The Hargrave/Rea hypothesis (1963) that southwestern wild turkeys are the descendents of feral domestics, rather than that Indian domestics were the descendents of indigenous wild forms.

Available data support this hypothesis. Rea (this vol.) has demonstrated that a different species of turkey was the indigenous inhabitant of most of the Southwest. Further, Merriam's Wild Turkey appeared in the Southwest subsequent to the spread of the Large Indian Domestic to which it is clearly related.

6. McKusick's hypothesis (1968) that turkeys were brought into the Southwest already domesticated from somewhere else as part of the Formative Cultural Complex.

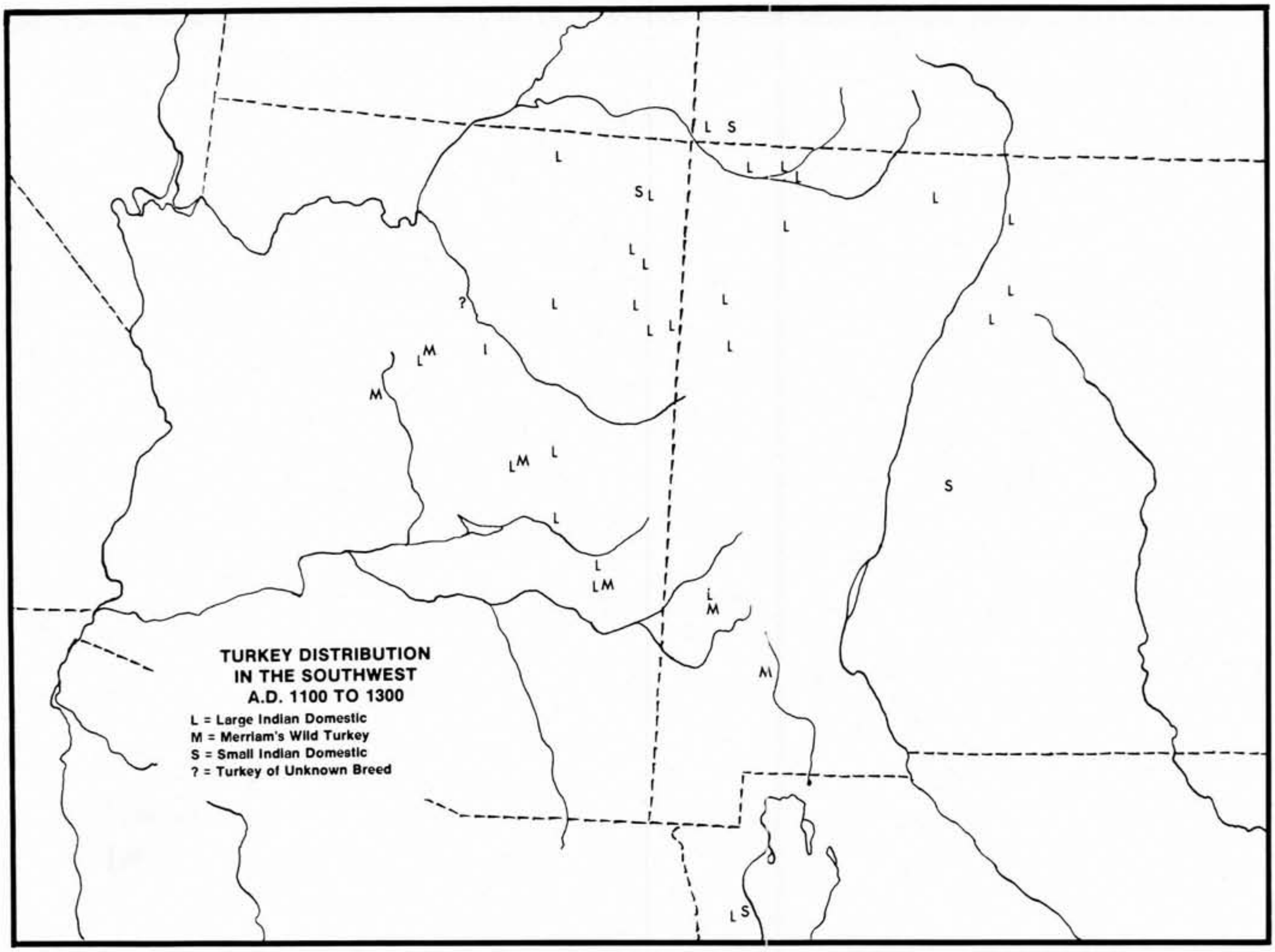

Figure 6. Turkey distribution in the Southwest from A.D. 1100 to 1300.

This hypothesis has also held up well. All early turkeys are identifiable as members of two well-standardized domestic breeds. The only evidence of local domestication in the Southwest is at Point of Pines, Arizona, where feral Large Indian Domestics (i.e., Merriam's Wild Turkeys) were apparently redomesticated.

No forms of *Meleagris gallopavo,* domestic or wild, are found in the Southwest proper before the advent of Formative Level Culture, first in the Mogollon Area, and much later, in the Anasazi Area. This is reasonable if one considers that the only way domestic turkeys could have been maintained in the circumstances in which they are known to have occurred is if there were a reliable agricultural surplus (Rea this vol.).

Where the domestics came from is still unknown. The Large Indian Domestics in their feral form did well in the mountains of the Mogollon Rim, but the Small Indian Domestics do not appear to have gone feral. Rea (pers. comm.) has suggested that this may indicate physiological as well as morphological differences between the Small and Large Indian Domestics, a possible result of the former having originally come from an area that was ecologically very different from the Southwest. The Small Indian Domestics were a small, dark-plumaged breed that, following Bergman's Rule and Allen's Rule (Van Tyne and Berger 1959:358), one would expect to inhabit a warm, moist environment. The arid Southwest was apparently inappropriate for their survival in the wild.

CONCLUSIONS

A review of the specimens of turkeys known to date from archaeological sites in the Southwest indicates that research into the origin and distribution of turkeys has been adversely affected by a basic misconception. The preconception that Indian turkeys were domesticated from birds native to the area has stood in the way of fruitful research for more than 40 years. Steadman (this vol.) and Rea (this vol.) have now corrected this misconception. The Indian domestics came from elsewhere, probably relatively far away, because the turkeys presently surrounding the area—the Rio Grande Turkey, *Meleagris gallopavo intermedia*; Gould's Wild Turkey, *M. g. mexicana*; and the South Mexican Turkey, *M. g. gallopavo*—are clearly not involved in the ancestry of the Small Indian Domestic, *M. g. tularosa,* and I am unable to find characters connecting any of them with the ancestry of the Large Indian Domestic, *M. g. merriami.*

As introduced domestics, Indian turkeys take on a different

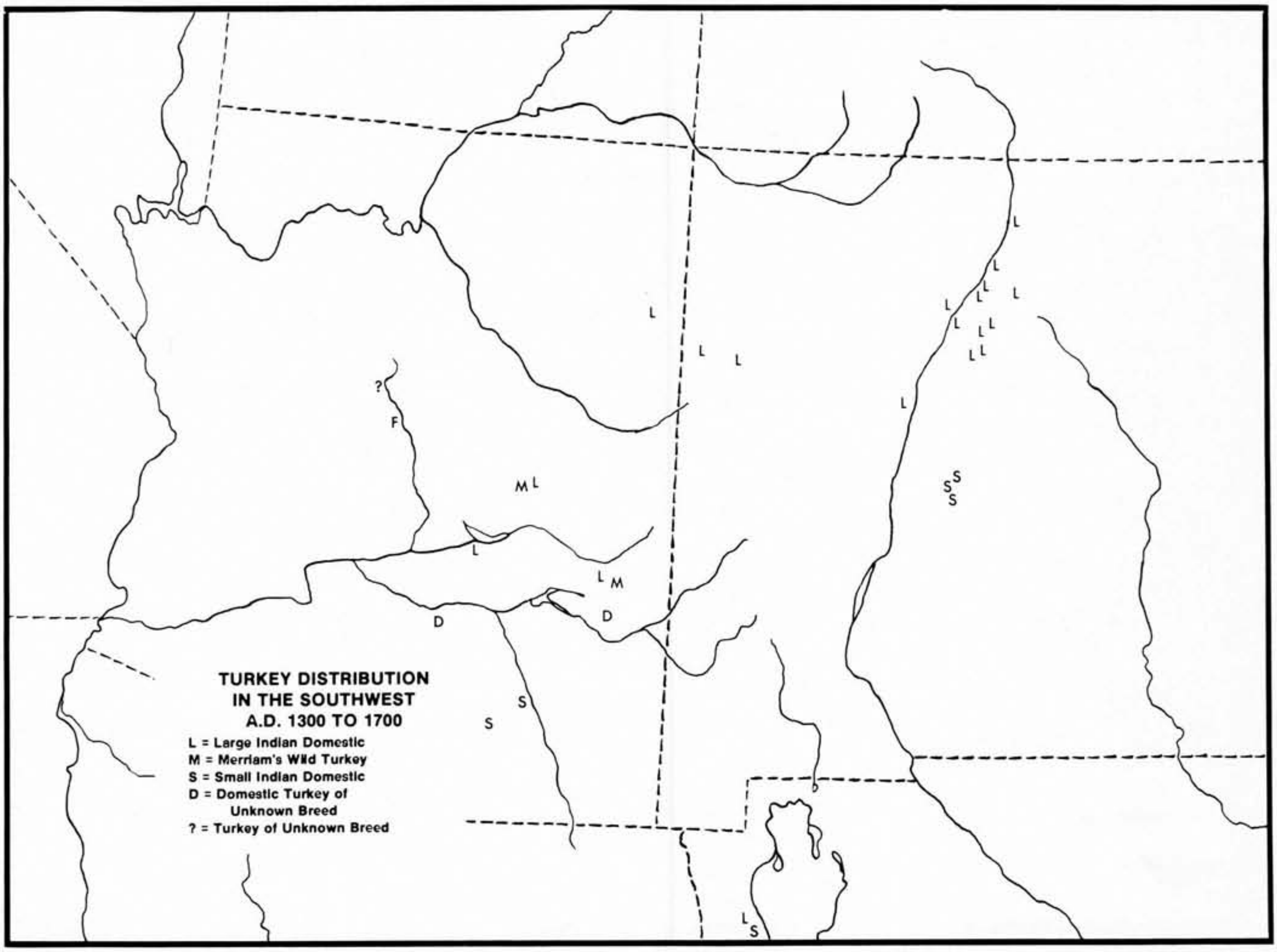

Figure 7. Turkey distribution in the Southwest from A.D. 1300 to 1700.

role than that to which the southwestern archaeologist has become accustomed. They are as characteristic of a people as are their pottery designs or their ceremonial paraphernalia. They are useful aids in tracing trade routes and movements of people. Their propagation and use is determined by cultural factors, not by ecological considerations.

The study of avian remains from southwestern sites began as an attempt to reconstruct prehistoric climate. Time and experience, however, have made it evident that certain portions of the avifauna are poor indicators of prehistoric climate. Southwestern Indians persistently went great distances, in some cases many hundreds of kilometers, to procure the birds they desired while ignoring locally available species. Therefore it is not surprising that the southwest Indians also brought domesticated turkeys from somewhere beyond the general area of their habitation.

The keeping of domestic turkeys presupposed a Formative State of Culture, when agriculture was already well enough established to provide a year-round surplus of food. In the Southwest, the Formative Stage is known earliest, about 300 B.C., in the Mogollon Area. As to be expected, the earliest turkeys in any southwest archaeological sites are also found in the Mogollon Area, as exemplified by the Small Indian Domestics at Tularosa Cave, that date from 300 B.C. ± 150 to 200 years. The next record of the Small Indian Domestic is at Canyon del Muerto, ca. A.D. 250, but the breed was not generally favored by the Anasazi, though a few apparently persisted at Antelope House through the Pueblo III occupation. On Mesa Verde, the few Small Indian Domestics present at Long House and Mug House date to ca. A.D. 1275 to 1300. At Casas Grandes, Chihuahua, Small Indian Domestics apparently interbred with Large Indian domestics. Why this hybridization should have occurred here is uncertain, but the peculiar nature of the site may shed some light on the problem. Casas Grandes, Chihuahua, was a trading outpost of Mesoamerica. Manufactured goods were produced and traded for raw materials and regional specialties. Turkeys from the American Southwest were apparently traded south in exchange for macaws. In the Mogollon and Anasazi Culture Areas, Small Indian Domestics and Large Indian Domestics co-existed for long periods without any discernable mixing, perhaps as the result of a cultural factor: that is, turkey strains may have been the property of kinship groups (in the same manner as, for example, seed corn), and may have been maintained as separate property. It may be that turkeys traded south to Casas Grandes entered a different cultural configuration, where they were merely merchandise, and where cultural factors that may have kept the strains separate in the north simply did not exist.

Small Indian Domestics were most numerous at the Tompiro Pueblos of central New Mexico. They were present there from ca. A.D. 1275 until the breed disappeared in A.D. 1672 with the fall of Las Humanas Pueblo at Gran Quivira National Monument.

The Large Indian Domestic appeared in the Southwest some time during the Basket Maker III Period, between A.D. 400 and 700. The vast number of turkey burials in Canyon del Muerto (Morris 1941), plus the rapidly increasing numbers of feather cord robes present in remains from the end of the previous period, suggest that a date of A.D. 400 to 500 for introduction of the breed is conservative. By A.D. 600 the Large Indian Domestic was already the most numerous turkey race in the Southwest. Its greatest areal expansion is coincidental with the Pueblo II Anasazi expansion that took place between A.D. 900 and 1100 (see Willey 1966:207, Fig. 5). Large Indian Domestics make up the greatest percentage of turkey remains at nearly all sites from A.D. 600 through 1672, when large flocks of domestic turkeys were last noted (Schroeder 1968:102–103).

Merriam's Wild Turkey was present by A.D. 600; it is not known before the time at which the Large Indian Domestic became the predominant southwestern breed. Analysis of plant remains from Tularosa Cave (Martin et al. 1952:469) outlines a regression of Mogollon Culture in the Georgetown Phase, A.D. 500 to 700, in which the Mogollon people dealt with some crisis in their way of life by retreating for 200 years into the Archaic Cultural Stage. Since we know that Indian domestic turkeys were already well established in their culture, it is reasonable to suppose that turkeys that may not have been adequately tended during this more mobile hunting and gathering period either died or became feral. No feral Tularosa Turkeys have ever been found, and the Small Indian Domestics that were not cared for probably died. However, feral Large Indian Domestics seem to have survived rather well, and are still with us today as Merriam's Wild Turkey.

The only experiment in turkey domestication that can be demonstrated in the entire Southwest, at any period, took place at Point of Pines, Arizona. There, at the base of Nantak Ridge, a classic population of Large Indian Domestics shows late admixtures of wild characters and an unprecedented increase in size. These fine big birds have been found at Casas Grandes, Chihuahua, and perhaps were traded for macaws, since macaws from AZ W:10:50 and Chih. D:9:1 show simultaneous identical abnormalities (McKusick 1974).

Thus, we have the Small Indian Domestic that may have persisted in small numbers for 1900 years, from as early as 300 B.C. to A.D. 1672; the Large Indian Domestic that was present in the Southwest for only about 1200 years, although in much greater numbers than the Small Indian Domestic; and the feral descendent of the Large Indian Domestic, Merriam's Wild Turkey, which has been around for 1400 years, and appears likely to persist given modern game management practices.

One factor that has become evident, but that was not considered in any of the hypotheses tested, is the relationship of the turkey to Mesoamerican socio-religious practices. While the occurrences of the macaw in the Southwest, both at Casas Grandes, Chihuahua, México, and in the United States, are recognized as a function of the ebb and flow of the popularity of the Quetzalcoatl Cult, little attention has been paid to the place of the turkey in this complex. Burland and Forman (1975:55–56) explain Quetzalcoatl, the Feathered Serpent, as the manifestation of the intellectual-conscious side of the human mind. However, Quetzalcoatl has a Dark Twin, Tezcatlipoca, The Smoking Mirror. The Smoking Mirror is made of polished obsidian and used for scrying (crystal-gazing as an aid to clairvoyance), thus Tezcatlipoca represents the intuitive-subconscious side of the human mind.

During the review of desiccated specimens of turkey remains for this paper, I found that there are several occurrences of the desiccated feet of turkeys that were tucked into dark corners of rock shelters, particularly in the area of Canyon de Chelley and Canyon del Muerto. Just as the macaw is the sign of Quetzalcoatl, so the turkey leg with claws is the sign of Tezcatlipoca (Burland and Forman 1975:61). These desiccated turkey feet date to ca. A.D. 1100, the point in time of the greatest frequency of macaw remains in the northern Southwest (Di Peso 1974). Certainly it would seem desirable to note occurrences of desiccated turkey feet from future excavations, like those from Tularosa Cave and the area of Canyon de Chelley and Canyon del Muerto to determine if other such parallels are present.

This reassessment of turkey remains from archaeological sites in the southwestern United States and some areas of México indicates three separate centers of turkey breeding:

1. The South Mexican, where domestic turkeys, *Meleagris gallopavo gallopavo,* were known in the Tehuacan Valley between A.D. 200 and 700 (McNeish 1964).
2. The Mogollon, where Small Indian Domestics, *Meleagris gallopavo tularosa,* were present between 300 B.C. ± 150 to 200 years.
3. The Anasazi, where Large Indian Domestics were probably present by A.D. 400 to 500.

Breeding per se was not successfully accomplished at all sites where turkey remains were found, and it was probably not even attempted at all sites. The frequency of turkey eggshells and small poults is highest at sites that could be considered trade centers. These are the same sites that yield such faunal remains as macaws, mountain lion and bear bones in ceremonial contexts, and human-bone artifacts. In most cases, neighboring smaller sites do not have eggshells or small poults. Presumably the birds were brought in as immatures from areas of specialization in turkey culture, at least from ca. A.D. 100 on.

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Thomas W. Mathews supervised the project for a period of 10 years, until the closing of the Southwest Archaeological Center, and contributed much to the analysis of the data. Chester A. Thomas provided time, funding, and travel arrangements during this period, and enlisted the assistance of the Gila County, Arizona, turkey hunters, without the cooperation of whom the project could not have been completed.

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UTILIZATION OF BIRDS BY THE ARCHAIC AND FREMONT CULTURAL GROUPS OF UTAH

By Paul W. Parmalee[1]

ABSTRACT: Approximately 5050 bird bones recovered from 5 Archaic and 11 Fremont sites in northern and western Utah were identified. Remains of a minimum of 1029 individuals, representing at least 21 families and 75 species, occurred in these prehistoric sites. Sixty-six percent of the elements identified were those of swans, geese, and ducks, thus indicating that species of waterfowl were the major supplemental avian food resources taken by these aboriginal people. Remains of aquatic and semi-aquatic birds comprised 90 percent of all elements recovered from these 16 sites. Some major wing and leg elements, especially those of large species (cranes, eagles, geese), were modified, suggesting a secondary use of birds as a bone resource for the manufacture of artifacts. Except for the Passenger Pigeon, *Ectopistes migratorius* (Linnaeus), all of the species represented in the archaeological samples still occur in Utah.

The prehistoric avifauna of Utah is poorly known, although large quantities of bird remains have been recovered during intensive archaeological investigations over the past four decades. This void has not resulted because of a lack of interest by archaeologists in this material, but rather because there are limited available comparative osteological collections and ornithologists/osteologists with time to devote to such studies. As has often been, and still is, the case, the archaeologist is faced with the problem of "farming out" much of the faunal material recovered during excavations. Archaeologically derived bird bones have not, for the most part, received much attention. However, there have been a few exceptions, notable among them the studies dealing with feather remains from Sand Dune Cave (Hargrave 1970) and Danger Cave (Sperry 1957), and bones from Hogup Cave (Parmalee 1970), the Levee and Knoll sites (Parmalee 1979), and the Bear River No. 2 site (Laybourne 1967).

The present study involves the analysis of approximately 5300 bird specimens from the collections of the Department of Anthropology, The University of Utah, Salt Lake City. These avian remains were recovered during site excavations by anthropology students and faculty at The University of Utah from the late 1930's to 1973 (Table 1). For various reasons, such as a lack of diagnostic ceramics or lithics, or because of occupation by two or more aboriginal groups, placement of each site within an exact cultural time sequence was not always possible. Based on all available cultural data, however, five of these sites have been determined by the archaeologists as being Archaic (ca. 7500–1000 B.C.) and 11 as having been occupied primarily by peoples of the Fremont culture (ca. A.D. 350–1450). Locations of the 16 sites are plotted in Figure 1.

The diversification of hunting practices among and within historic Indian tribes of North America has been well documented in the ethnographic literature. Hunting activities were carried out either by individuals, by family groups, or as a communal effort, depending upon the types of game sought, its availability at a particular season (e.g., waterfowl migrations and major bison herd movements), and/or the use of appropriate techniques that would provide the greatest yield. The species of birds hunted also varied considerably within and among tribes. Weisel (1952:348) stated that "The Flathead ate all the birds and their eggs," although individuals of most tribes for which there are subsistence data exhibited distinct preferences for certain species while refusing to eat others. Judd (1954:266), in commenting on a list of 13 species of birds identified from osteological remains recovered at Pueblo Bonito, New Mexico, suggested that "Presumably these were killed or kept captive for their feathers alone, since the Pueblos have always shunned winged creatures as a source of food." The southern Paiute were reported to have eaten "many kinds" of birds (Kelly 1964:53, 54), but they would not eat crows, certain woodpeckers, and meadowlarks. Mandelbaum (1940:199) presented a list of avian species, compiled from data obtained from tribal informants, that were and were not hunted for food by the Plains Cree. It is of interest to note that these people would eat the young of some species, e.g., crows and ravens, but not the adults.

Kelly (1964:53) stated that "most birds [were] taken from blind . . . usually shot," [southern Paiute]. "The boys [Hidatsa, North Dakota] practice themselves in the use of the bow by shooting at marmots and small birds, and in winter they set horse-hair snares for snow-buntings" (Matthews 1877:58). Lowie (1909:185), in discussing the northern Shoshone, mentioned that "Sage-hens were driven into an enclosure, or trapped with nooses." He also described (Lowie 1924:197) the elaborate communal hunt for ducks and "mud-hens." In contrast, Steward (1933:255) makes the following comment on the

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Table 1. Data relative to Utah archaeological sites from which avifaunas were recovered.

Site Name and Designation	Utah County	Year Excavated	Cultural Designation (C14 Dates)	Locale	Published References
Deadman Cave 42TO64	Tooele	1938	Archaic	NE Slope Oquirrh Mts. Great Salt Lake	Smith, E.R. 1952
Stansbury I 42TO1	Tooele	1947	Archaic	N. Facing Slope, Stansbury Is. Great Salt Lake	Jameson, S.J.S. 1958
Stansbury II 42TO2	Tooele	1947	Archaic	N. Facing Slope, Stansbury Is. Great Salt Lake	Jameson, S.J.S. 1958
Sandwich Shelter 42TO108	Tooele	1969	Archaic 7040 ± 280 BP	Alcove, Flank of Stansbury Mts. Great Salt Lake	Marwitt, J.P., G.F. Frye, and J.M. Adovasio 1971
Black Rock II 42TO29	Tooele	1938	Archaic	N. Slope Oquirrh Mts. Great Salt Lake	—
Black Rock III 42TO3	Tooele	1939	Fremont	N. Slope Oquirrh Mts. Great Salt Lake	Enger, W.D., Jr. 1942
Bear River No. 1 42BO55	Box Elder	1964	Fremont AD 885 ± 120	Marshy River Bank Bear River	Aikens, C.M. 1966
Bear River No. 3 42BO98	Box Elder	1967	Fremont AD 500 ± 110	Marshy River Bank Bear River	Shields, W.F., and G.F. Dalley 1978
Levee 42BO107	Box Elder	1969	Fremont AD 700 ± 140	Marshy Lake Side Klondike Lake/ Bear River	Parmalee, P.W. 1979
Knoll 42BO109	Box Elder	1969	Fremont AD 1310 ± 110	Marshy Lake Side Klondike Lake/ Bear River	Parmalee, P.W. 1979
Warren 42WB-	Weber	1946	Fremont	Near Mouth of Warren River	Enger, W.D., Jr., and W. Blair 1947
Injun Creek 42WB34	Weber	1965	Fremont AD 1605 ± 100 AD 1365 ± 90	Alluvium, Weber River Delta, Injun Creek Marsh	Aikens, C.M. 1966
Unnamed 42SL19	Salt Lake	1961	Fremont	Foothills Wasatch Mts. Jordon River	—
Nephi 42JB2	Juab	1965–1966	Fremont AD 780 ± 85 AD 1670 ± 80	Alluvial Fan; Salt Creek Drainage	Sharrock, F.W., and J.P. Marwitt 1967
Evans Mound 42IN40	Iron	1970–1973	Fremont AD 1095 ± 90	Parowan Valley Alluvial Fan, Summit Creek	Berry, M.S. 1972
Pharo Village 42MD180	Millard	1967	Fremont AD 460 ± 80 AD 1260 ± 90	Alluvial Fan, Base of Pavant Mts. Pharo Creek	Marwitt, J.P. 1968

manner of taking waterfowl by the Owens Valley Paiute (Nevada): "Killed in early morning by hunters concealed in blinds resembling wickiups or summer houses. Decoys, nets, and communal hunts were unknown." It is apparent from these few ethnographic accounts that great variability in hunting practices and the species of birds used did exist among contemporaneous aboriginal groups during the early historic period. Therefore, interpretation of osteological avian remains relative to the possible methods of capturing birds and the preference for or use of certain species by *prehistoric* peoples is basically speculative.

Hayward et al. (1976:25) pointed out that "Since birds are among the most mobile of vertebrates, it is difficult to define many of them in terms of their confinement to any special community." Although a large portion of Utah is desert, receiving rarely more than 25 cm of annual precipitation, the state possesses both salt and freshwater lakes as well as a series of high mountain ranges, plateaus, and major river systems (e.g., the Bear, Provo, Green, and Colorado) that provide diverse avian habitats. Aboriginals occupying camp sites and villages established along the larger rivers, mountain streams, or lakes had available to them not only the aquatic species

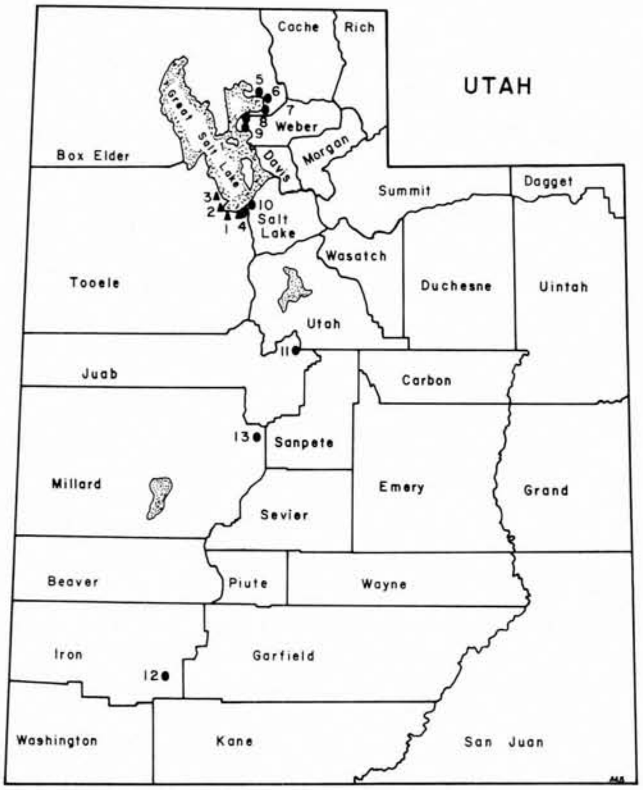

Figure 1. Location of Archaic (triangles) and Fremont (circles) sites from which avian specimens were obtained and examined for this study. Deadman Cave (1), Stansbury I and II (2), Sandwich Shelter (3), Black Rock II and III (4), Bear River No. 1 and No. 3 (5), Levee (6), Knoll (7), Warren (8), Injun Creek (9), Unnamed (10), Nephi (11), Evans Mound (12), Pharo Village (13).

that inhabited these bodies of water and the adjacent marshlands or riparian habitat, but also upland birds (e.g., Sage Grouse) that occurred in the bordering dry brushlands and desert. Faunal assemblages from archaeological sites in Utah reflect the Indian's exploitation of these varied habitats or biomes.

Environmental changes that have occurred since portions of northern and western Utah were covered with ancient Lake Bonneville are difficult to define and, thus far, none of major impact have been reflected in the animal remains recovered from archaeological sites. Durrant (1970:241, 245) comments on this problem in describing the mammalian fauna from the Archaic Hogup Cave site (Box Elder County, northwestern Utah) and discusses factors that affect interpretation of archaeologically derived faunal material: "Based upon osteological remains representing 3,440 individual animals, it is evident that the mammalian fauna of the Hogup Cave area throughout Neothermal time was remarkably uniform and similar to that found there today. This indicates that, with some fluctuations, there existed a certain similarity in environmental factors throughout these past nine millenia. The data lead me to consider that the climate of the Hogup area during Neothermal time was somewhat cooler in the early Anathermal period, then became gradually warmer, reaching a moderately high temperature during the Altithermal, and then gradually cooled through the Medithermal to the present. In addition to the lack of significant qualitative differences within the fauna over time, another factor contributing to uncertainty in interpretation is that, although it is known that the cave vicinity was an autumnal harvesting area for its aboriginal occupants, no one knows either the range of these people in their hunting forays and migrations or the number of persons involved. Moreover, no data are available on the cyclic patterns of the mammals of that time, and certain mammals occur together in the cave deposits that occupy somewhat discrete ranges at present. Inferences concerning past climatic conditions in the area of Hogup Cave cannot be made easily from the data currently at hand. The tendency of man to engage in selective hunting and gathering and to transport items long distances greatly complicates interpretation. Certainly the deposits offer little evidence for sudden and dramatic changes in either vegetation or fauna with the onset of the Altithermal."

In the faunal assemblage from Hogup Cave and other Archaic sites, e.g., Danger Cave (Jennings 1957), remains of ungulates, especially the Pronghorn (*Antilocapra americana* (Ord)), and rabbits (*Lepus* Linnaeus and *Sylvilagus* Gray) predominated. Although the Bison, *Bison bison* (Linnaeus), was taken by Archaic peoples, it was not until the later Fremont cultural period that it became the dominant protein source. Also, as Jennings (1978:233) has pointed out, ". . . all the local variations in favored game do not obscure what seems to be a Fremont preference for mule deer where ever it is available. The adaptability in choice of game may then be toward substitution when deer is rare—a reasonable and expectable adjustment." The Archaic populations of the Great Basin appear to have been geared to a mobile hunting-collecting way of life, while the Fremont people, an apparent cultural derivative from the earlier Desert Archaic, were more sedentary and partly or perhaps predominantly agricultural. Although hunting and trapping techniques may have varied between the Archaic and Fremont peoples, both groups relied heavily on the endemic fauna, especially mammals, as a primary food resource. From a strictly "pounds of derived meat" point of view, birds must be considered as a supplemental food resource in the total food economy of these people, but undoubtedly one that was of periodic significance.

MATERIAL AND METHODS

A combined total of about 5300 bird bones from 16 archaeological sites were examined and, of this number, 5043 or about 95 percent were identifiable to family, genera, and/or species. At least 75 species from 21 families occurred in the combined samples. Avian osteological collections housed in the Zoology Section, Illinois State Museum, Springfield, and in the Zooarchaeology Section, Department of Anthropology, The University of Tennessee, Knoxville, were used in connection with this study. *Utah Birds* by Behle and Perry (1975) and *Birds of Utah* by Hayward et al. (1976) are cited as the latest comprehensive authorities on the known distribution and abundance of birds in the state.

Analysis of archaeologically derived avian bone samples often must be conservative because of the innumerable variables and unknown factors affecting each sample and each site. In attempting to compare past avian assemblages and their use by aboriginal man, in this case between Archaic and Fremont peoples, the inequality of sample size may be a sig-

Table 2. Birds identified from Archaic and Fremont Sites in Utah, with number of specimens and minimum number of individuals (given in parentheses).

Species	Deadman Cave 42TO64	Stansbury I 42TO1	Stansbury II 42TO2	Sandwich Shelter 42TO 108	Black Rock II 42TO29	Black Rock III 42TO3	Bear River No. 1 42BO55	Bear River No. 3 42BO98
Family Podicipedidae—Grebes								
Eared Grebe, *Podiceps nigricollis*	2 (1)	24 (13)	30 (6)	287 (46)	16 (10)			1 (1)
Western Grebe, *Aechmorphorus occidentalis*							1 (1)	
Pied-billed Grebe, *Podilymbus podiceps*							1 (1	
Grebe sp.				122				
Family Pelecanidae—Pelicans								
White Pelican, *Pelecanus erythrorhynchos*	3 (1)			6 (1)			13 (4)	133 (10)
Family Phalacrocoracidae—Cormorants								
Double-crested Cormorant, *Phalacrocorax auritus*	1 (1)							
Family Ardeidae—Herons and Bitterns								
Great Blue Heron, *Ardea herodias*	2 (1)				1 (1)			3 (1)
Little Blue Heron, *Egretta caerulea*					1 (1)			
Common Egret, *Egretta alba*	1 (1)						3 (1)	8 (2)
Snowy Egret, *Egretta thula*							1 (1)	
Black-crowned Night Heron, *Nycticorax nycticorax*	1 (1)							3 (1)
American Bittern, *Botaurus lentiginosus*							9 (4)	15 (5)
Heron sp.	3 (1)							
Family Plataleidae—Ibises and Spoonbills								
White-faced Ibis, *Plegadis chihi*								
Family Anatidae—Swans, Geese and Ducks								
Whistling Swan, *Olor columbianus*							3 (1)	
Trumpeter Swan, *Olor buccinator*							2 (1)	
Swan, *Olor* sp.							2 (1)	6 (3)
Canada Goose, *Branta canadensis*	103 (13)		1 (1)	2 (1)	1 (1)	3 (1)	18 (3)	59 (8)
Snow Goose, *Chen caerulescens*	244 (26)	1 (1)			2 (2)	2 (1)		25 (5)
Ross' Goose, *Chen rossii*								
Goose, sp.	146					3	20	37
Mallard, *Anas platyrhynchos,* and/or Black Duck, *Anas rubripes*	79 (24)		1 (1)	1 (1)	9 (3)	2 (1)	35 (9)	97 (28)
Gadwall, *Anas strepera*	2 (1)						4 (4)	2 (1)
Pintail, *Anas acuta*	7 (3)					1 (1)	8 (6)	9 (4)
Mallard/Black Duck/Pintail group, *Anas* spp.			1 (1)		8 (2)	2 (1)	60 (12)	48 (7)
Green-winged Teal, *Anas crecca*	2 (2)				16 (9)	1 (1)	16 (10)	22 (9)
Blue-winged Teal, *Anas discors,* and/or Cinnamon Teal, *Anas cyanoptera*	1 (1)				2 (1)		5 (3)	3 (2)
Teal, *Anas* sp.	3 (2)				20 (5)		22 (5)	24 (3)
Wigeon, *Anas* cf. *americana*	2 (1)						6 (5)	2 (2)
Shoveler, *Anas clypeata*	2 (1)						7 (2)	4 (2)
?Wood Duck, *Aix sponsa*								
Redhead, *Aythya americana*							6 (2)	1 (1)
Ring-necked Duck, *Aythya collaris,* and/or Lesser Scaup, *Aythya affinis*							13 (2)	7 (2)
Canvasback, *Aythya valisineria*							3 (1)	6 (2)
Duck, *Aythya* sp.								
Goldeneye, *Bucephala* sp.								2 (1)
Bufflehead, *Bucephala albeola*					2 (1)		2 (1)	2 (1)
Ruddy Duck, *Oxyura jamaicensis*	1 (1)			1 (1)			3 (1)	1 (1)
Duck sp.	85		2		17	3	79	183
Hooded Merganser, *Lophodytes cucullatus*								
cf. Common Merganser, *Mergus merganser*	1 (1)							15 (4)
cf. Red-breasted Merganser, *Mergus serrator*								3 (2)
Merganser, *Mergus* sp.							18 (3)	
Family Accipitridae—Hawks and Harriers								
cf. Red-tailed Hawk, *Buteo jamaicensis*								
Swainson's Hawk, *Buteo swainsoni,* and/or Rough-legged Hawk, *Buteo lagopus*			7 (2)			2 (1)	1 (1)	

Table 2. Continued.

Levee 42BO107	Knoll 42BO109	Warren 42WB-	Injun Creek 42WB34	Un-named 42SL19	Nephi 42JB2	Evans Mound 42IN40	Pharo Village 40MD180	Total No. Specimens	Per-cent of Speci-mens
								500 (86)	9.92
		2 (2)	2 (1)	1 (1)			1 (1)	366 (82)	7.26
								1 (1)	0.02
10 (2)								11 (3)	0.22
								122	2.42
								242 (27)	4.80
69 (5)	15 (3)		1 (1)	1 (1)	1 (1)			242 (27)	4.80
								22 (5)	0.44
20 (3)			1 (1)					22 (5)	0.44
								115 (37)	2.29
								6 (3)	0.12
								1 (1)	0.02
11 (2)								23 (6)	0.46
8 (5)								9 (6)	0.18
								4 (2)	0.08
43 (7)			1 (1)					68 (17)	1.35
					1 (1)			4 (2)	0.08
								1 (1)	0.02
1 (1)								1 (1)	0.02
								3347 (611)	66.40
					1 (1)	2 (1)		6 (3)	0.12
				2 (1)	1 (1)			5 (3)	0.10
								8 (4)	0.16
29 (7)	12 (3)	13 (3)	69 (11)	2 (2)				312 (54)	6.19
114 (18)	38 (7)	8 (2)	6 (2)		1 (1)			441 (65)	8.74
3 (2)	10 (5)							13 (7)	0.26
28	6	6	54	2				302	5.99
94 (27)	16 (5)	10 (3)	23 (5)	4 (1)	11 (3)	2 (1)	21 (4)	405 (116)	8.03
11 (4)	5 (2)	1 (1)	1 (1)					26 (14)	0.52
25 (9)	11 (4)	2 (2)	7 (3)					70 (32)	1.39
61 (10)	6 (2)	13 (7)	31 (8)	2 (1)	9 (2)			241 (53)	4.78
45 (13)	1 (1)	4 (3)		1 (1)	4 (1)			112 (50)	2.22
13 (7)		2 (1)	2 (1)	1 (1)	2 (1)		9 (4)	40 (22)	0.79
117 (14)	2 (1)		4 (2)					192 (32)	3.81
5 (4)	1 (1)	1 (1)		1 (1)				18 (15)	0.36
22 (9)	4 (2)	1 (1)	1 (1)					41 (18)	0.81
2 (2)								2 (2)	0.04
12 (4)		1 (1)	1 (1)				2 (1)	23 (10)	0.46
20 (5)		3 (1)	59 (12)		4 (2)		1 (1)	107 (25)	2.12
5 (2)			2 (1)					16 (6)	0.32
24 (10)	1 (1)		2 (1)					27 (12)	0.54
2 (1)			3 (3)					7 (5)	0.14
7 (3)			6 (4)					19 (10)	0.38
14 (4)		1 (1)	1 (1)	1 (1)			1 (1)	24 (12)	0.48
223	11		122	5	8		22	760	15.07
	1 (1)							1 (1)	0.02
2 (2)								18 (7)	0.36
2 (2)	1 (1)							6 (5)	0.12
71 (17)	4 (2)	4 (1)	2 (1)	3 (1)	2 (2)		1 (1)	105 (28)	2.08
								67 (34)	1.34
							1 (1)	1 (1)	0.02
			4 (1)			7 (2)		21 (7)	0.42

Continued

Table 2. Continued.

Species	Deadman Cave 42TO64	Stansbury I 42TO1	Stansbury II 42TO2	Sandwich Shelter 42TO 108	Black Rock II 42TO29	Black Rock III 42TO3	Bear River No. 1 42BO55	Bear River No. 3 42BO98
Hawk, *Buteo* sp.								
Hawk, sp.	2 (1)				1 (1)			
Golden Eagle, *Aquila chrysaetos*	1 (1)						1 (1)	
Bald Eagle, *Haliaeetus leucocephalus*	1 (1)							
Eagle sp.								
Marsh Hawk, *Circus cyaneus*	7 (2)						2 (2)	1 (1)
Family Falconidae—Falcons								
Prairie Falcon, *Falco mexicanus*								
Peregrine Falcon, *Falco peregrinus*	6 (2)							1 (1)
Falcon, *Falco* sp.					3 (2)			
Kestrel, *Falco sparverius*								
Family Tetraonidae—Grouse and Ptarmigan								
Blue Grouse, *Dendragapus obscurus*	5 (2)				9 (2)		1 (1)	
Ruffed Grouse, *Bonasa umbellus*	4 (1)							
Sharp-tailed Grouse, *Pedioecetes phasianellus*					3 (2)		3 (1)	
Sage Grouse, *Centrocercus urophasianus*	10 (2)			1 (1)	9 (3)		1 (1)	
Grouse sp.					7		2	
Family Gruidae—Cranes								
Sandhill Crane, *Grus canadensis*	30 (4)							
Family Rallidae—Rails, Gallinules & Coots								
Sora, *Porzana carolina*								
cf. Purple Gallinule, *Porphyrula martinica*								
American Coot, *Fulica americana*	1 (1)			1 (1)	1 (1)		6 (3)	25 (5)
Family Charadriidae—Plovers and Turnstones								
Black-bellied Plover, *Pluvialis squatarola*								2 (1)
Family Scolopacidae—Snipe and Sandpipers								
Common Snipe, *Capella gallinago*								1 (1)
Long-billed Curlew, *Numenius americanus*	4 (3)				4 (1)			
Willet, *Catoptrophorus semipalmatus*								
cf. Greater Yellowlegs, *Tringa melanoleucus*							1 (1)	
Family Recurvirostridae—Avocets and Stilts								
American Avocet, *Recurvirostra americana*	1 (1)				4 (1)		4 (1)	4 (1)
Black-necked Stilt, *Himantopus mexicanus*								
Family Stercorariidae—Jaegers and Skuas								
cf. Parasitic Jaeger, *Stercorarius parasiticus*					1 (1)			
Family Laridae—Gulls and Terns								
cf. California Gull, *Larus californicus*	4 (1)							
Gull, *Larus* sp.		2 (1)	6 (2)	3 (1)	1 (1)			
cf. Caspian Tern, *Hydroprogne caspia*	1 (1)							
Family Columbidae—Pigeons and Doves								
Passenger Pigeon, *Ectopistes migratorius*			1 (1)					
Mourning Dove, *Zenaidura macroura*			1 (1)					
Family Strigidae—Owls								
Great Horned Owl, *Bubo virginianus*	7 (2)		1 (1)	3 (2)	2 (1)	2 (1)		
Burrowing Owl, *Speotyto cunicularia*	1 (1)							
Spotted Owl, *Strix occidentalis*								
Long-eared Owl, *Asio otus*, and/or Short-eared Owl, *Asio flammeus*	3 (1)			1 (1)	5 (3)			5 (3)
Family Picidae—Woodpeckers								
Common Flicker, *Colaptes auratus*	1 (1)			1 (1)	1 (1)			
Family Corvidae—Jays, Magpies and Crows								
Black-billed Magpie, *Pica pica*					1 (1)		1 (1)	
Common Raven, *Corvus corax*	12 (5)	1 (1)	7 (3)	8 (2)	22 (4)		4 (2)	2 (1)
Clark's Nutcracker, *Nucifraga columbiana*								

Table 2. Continued.

Levee 42BO107	Knoll 42BO109	Warren 42WB-	Injun Creek 42WB34	Un-named 42SL19	Nephi 42JB2	Evans Mound 42IN40	Pharo Village 40MD180	Total No. Specimens	Per-cent of Speci-mens
					1 (1)	4 (3)	4 (2)	9 (6)	0.18
1 (1)			1 (1)			2 (1)		7 (5)	0.14
			1 (1)	2 (1)			1 (1)	6 (5)	0.12
								1 (1)	0.02
			1					1	0.02
5 (1)	1 (1)	1 (1)	3 (1)				1 (1)	21 (9)	0.42
								23 (14)	0.46
1 (1)	1 (1)							2 (2)	0.04
							2 (2)	9 (5)	0.18
				1 (1)	3 (2)	2 (1)	1 (1)	10 (7)	0.20
						2 (1)		2 (1)	0.04
								287 (50)	5.70
					17 (4)	2 (1)	76 (10)	110 (20)	2.18
							9 (4)	13 (5)	0.26
1 (1)		1 (1)	5 (1)	1 (1)	3 (1)		12 (3)	29 (11)	0.58
4 (1)					8 (2)	11 (2)	6 (2)	50 (14)	0.99
3			2		11	2	58	85	1.69
								37 (7)	0.73
			1 (1)				6 (2)	37 (7)	0.73
								146 (37)	2.90
			1 (1)					1 (1)	0.02
6 (2)								6 (2)	0.12
76 (11)		4 (1)	2 (2)	2 (1)		4 (2)	17 (6)	139 (34)	2.76
								2 (1)	0.04
								2 (1)	0.04
								21 (15)	0.42
								1 (1)	0.02
	2 (1)	2 (2)	1 (1)		1 (1)			14 (9)	0.28
2 (1)	1 (1)							3 (2)	0.06
2 (2)								3 (3)	0.06
								32 (12)	0.63
16 (5)		2 (2)						31 (11)	0.61
1 (1)								1 (1)	0.02
								1 (1)	0.02
								1 (1)	0.02
								28 (12)	0.56
								4 (1)	0.08
2 (1)	1 (1)		7 (2)					22 (9)	0.44
	1 (1)							2 (2)	0.04
								4 (4)	0.08
								1 (1)	0.02
					2 (2)			3 (3)	0.06
								54 (26)	1.08
			4 (1)	1 (1)		5 (1)	3 (1)	28 (11)	0.56
					1 (1)	2 (1)		4 (3)	0.08
							1 (1)	1 (1)	0.02
4 (1)			2 (1)		1 (1)			21 (11)	0.42
								4 (4)	0.08
			1 (1)					4 (4)	0.08
								96 (33)	1.91
			2 (1)		1 (1)	2 (1)		7 (5)	0.14
3 (1)	2 (1)		9 (3)		6 (2)	11 (2)		87 (27)	1.73
							2 (1)	2 (1)	0.04

Continued

Table 2. Continued.

Species	Deadman Cave 42TO64	Stans-bury I 42TO1	Stans-bury II 42TO2	Sand-wich Shelter 42TO 108	Black Rock II 42TO29	Black Rock III 42TO3	Bear River No. 1 42BO55	Bear River No. 3 42BO98
Family Icteridae—Meadowlarks, Orioles and Blackbirds								
Western Meadowlark, *Sturnella neglecta*			1 (1)	1 (1)	1 (1)			
Yellow-headed Blackbird, *Xanthocephalus xanthocephalus*								
Red-winged Blackbird, *Agelaius phoeniceus*								1 (1)
Order Passeriformes—Perching Birds								
Indet. Passerines			5 (4)					
TOTAL	792 (116)	28 (16)	59 (20)	443 (64)	170 (62)	21 (8)	387 (98)	763 (123)

nificant factor. Little or nothing is known of early hunting techniques. One group may have devised a method of capturing grebes while another learned how to efficiently hunt pelicans, yet both birds may have been present as a potentially abundant food resource. The role birds played in the total subsistence economy is often problematical; Sharrock and Marwitt (1967:39) and others have commented that, as a group, birds were at best of only secondary importance as a food resource in comparison to mammals. It would require a large number of grebes or ducks to equal the actual number of kilos of usable meat derived from an adult deer or bison, for example. Nevertheless, the value of birds as a constant or seasonal supplemental food resource cannot be discounted. Although all species of birds are edible, individual or tribal preference for or against the taking of a particular species or group of birds is yet another factor affecting an interpretative analysis of any given faunal sample.

The bird bones examined were well preserved and in a great many instances complete. However, intraspecific osteological variation because of sex, age, or individual variation often make species determinations uncertain or impossible. For this reason, and because some elements were broken and/or nondiagnostic, many identifications could not be accurately carried beyond a general group level (e.g., Duck sp.; Hawk sp.; Duck, *Aythya* sp.; Table 2). Identification of similar sized specimens of closely related species within a particular genus is also difficult and often limited, depending on the elements with which one must work.

Remains of swans, geese, and ducks totaled 3347, 66 percent of all elements identified (Table 3). In addition to the "usual" problems of identification, the high incidence of hybridization among members of the Anatidae and other families (e.g., the Parulidae) may further complicate attempts to arrive at some species determinations. Johnsgard (1960:25) has commented that ". . . waterfowl of the family Anatidae have provided the greatest number and variety of bird hybrids originating from both natural and captive conditions." Not only have fertile hybrids resulted between species within the same genus (e.g., Mallard × Pintail), but also between species of different genera (Mallard × Common Merganser). I know of no study on the osteology of hybrid ducks and geese. It is not inconceivable that some "problem" waterfowl elements from aboriginal sites could well have come from hybrids. In spite of certain basic identification problems and the use of tentative determinations in some instances, interesting and useful data have come to light concerning the overall use of birds in the food economy of aboriginal man in Utah.

ACCOUNTS OF SPECIES

Family Podicipedidae—Grebes

The contrast in the utilization of grebes between Archaic and Fremont peoples who occupied sites bordering the Great Salt Lake is striking. About 32 percent of all bird remains from the Archaic sites were those of grebes, the majority of elements occurring in Sandwich Shelter (Table 2). A total of 287 bones (46 individuals) were identified as the Eared Grebe, *Podiceps nigricollis* Brehm, a common summer resident in marshes along the east side of Great Salt Lake (Behle and Perry 1975). The 122 indeterminate grebe elements, which are probably also those of *P. nigricollis,* bring the total number of grebe bones from this one site to slightly over 400. In contrast, only 19 grebe elements were recovered from all 11 Fremont sites. The reason(s) for this apparent differential use of grebes between cultural groups is unclear, as is the paucity of remains of the Pied-billed Grebe, *Podilymbus podiceps* (Linnaeus), and the Western Grebe, *Aechmorphorus occidentalis* (Lawrence)—two species that are also common summer residents in the Great Salt Lake.

Family Pelecanidae—Pelicans

Elements of the White Pelican, *Pelecanus erythrorhynchos* Gmelin, comprised 6.5 percent of all remains from the Fremont site samples, but less than 1 percent of those from the Archaic sites. The large size of this bird would presumably have made it a desirable food resource, yet less than 30 individuals are represented in the combined faunal assemblages. It is currently a common summer resident of the Great Salt Lake with a breeding colony at Gunnison Island (Behle and Perry 1975). None of the elements were from nestlings or fledglings.

Table 2. Continued.

Levee 42BO107	Knoll 42BO109	Warren 42WB-	Injun Creek 42WB34	Un-named 42SL19	Nephi 42JB2	Evans Mound 42IN40	Pharo Village 40MD180	Total No. Specimens	Per-cent of Speci-mens
								9 (8)	0.18
					1 (1)			4 (4)	0.08
3 (2)								3 (2)	0.06
			1 (1)					2 (2)	0.04
								5 (4)	0.10
								5 (4)	0.10
1243 (233)	154 (48)	82 (37)	449 (82)	33 (17)	101 (35)	60 (20)	258 (51)	5043 (1030)	100.1

Family Phalacrocoracidae—Cormorants

Behle and Perry (1975) list the Double-crested Cormorant, *Phalacrocorax auritus* (Lesson), as an uncommon summer resident in northern Utah, and a transient and rare winter visitant throughout the state. If this species occurred in greater numbers in prehistoric times, the Indian made little use of it. Remains of *P. auritus* occurred in only three sites: one element each at the Deadman Cave and Injun Creek sites and 20 (three individuals) at the Levee site.

Family Ardeidae—Herons and Bitterns

Six species representative of this family were identified from the faunal samples; 90 percent of the remains occurred in Bear River Nos. 1 and 3 and Levee, sites once located on the marshy shore of Great Salt Lake. Specimens of the Great Blue Heron (*Ardea herodias* Linnaeus), Snowy Egret (*Egretta thula* (Molina)), Black-crowned Night Heron (*Nycticorax nycticorax* (Linnaeus)), and American Bittern (*Botaurus lentiginosus* (Rackett)), reported as common summer residents in northern Utah by Behle and Perry (1975), are not unexpected at sites once located in habitat well suited for these wading birds. A proximal right humerus from Black Rock II compared closely with the Little Blue Heron, *Egretta caerulea* (Linnaeus), a species of only occasional occurrence in Utah. The Common Egret, *E. alba* (Linnaeus), is considered a rare transient, but remains of this large, showy species were recovered at four sites and represented a minimum of six individuals. Laybourne (1967) reported four elements of *E. alba* from Bear River No. 2. Although of potential food value, these birds may also have been prized especially for their plumage. Three bones from a nestling heron or bittern occurred in the faunal sample from Deadman Cave.

Family Plataleidae—Ibises and Spoonbills

The White-faced Ibis, *Plegadis chihi* (Vieillot), today is a "Common summer resident in Great Salt Lake marshes" (Behle and Perry 1975), and in view of this the recovery of only one specimen, a complete right humerus from the Levee site, is surprising. Hayward et al. (1976:46) mentioned a comment by Allen (1872:172), who stated that the White-faced Ibis was reported to have ". . . become numerous only during the last two or three years," but no reason for its apparent increase was offered. It is evident that the Indian hunted the marshes for herons, bitterns, and other semi-aquatic species, and it seems unlikely that there would have been a taboo against taking this ibis, so the single record may suggest that *P. chihi* was a rare species in the vicinity of the Great Salt Lake during early prehistoric times.

Family Anatidae—Swans, Geese, and Ducks

At least 22 species of waterfowl were represented in the faunal samples, and their remains made up about 66 percent of the total sample. Elements of these birds constituted approximately 51 percent of all avian remains from the Archaic sites and 73 percent from the Fremont sites (Tables 2 and 3). Bones of waterfowl constituted 66 percent of the avifauna reported by Parmalee (1970) from Hogup Cave, an Archaic site located about 25 km west of the Great Salt Lake, and 85 percent of the bird remains identified from the Bear River No. 2 site (Fremont) by Laybourne (1967) were those of waterfowl. It can be presumed, on the basis of these percentages and the variety and number of species they represent, that waterfowl, especially geese and ducks, were often hunted and formed a valuable supplement in the food economy of these people.

Although the Whistling Swan, *Olor columbianus* (Ord), occasionally occurs in large concentrations in marshes adjacent to the Great Salt Lake, and the Trumpeter Swan, *Olor buccinator* Richardson, was formerly more common (now occasional) in northern Utah (Behle and Perry 1975), the Indians who occupied these areas rarely took either species. Remains of one or both swans were identified from five of the Fremont sites, and both are recorded by Laybourne (1967) from Bear River No. 2, but no more than six elements were identified from any one site. Elements of geese, however, were especially numerous and the number of geese specimens represented 21 percent of the total. A large subspecies of the Canada Goose, *Branta canadensis moffitti* Aldrich, is a common resident of the Great Salt Lake (Behle and Perry 1975) and at least three other races occur in Utah as transients. With the possible exception of the giant Canada Goose, *B. c. maxima* Delacour, and Hutchins' Goose, *B. c. hutchinsii* (Richardson), it is im-

Table 3. Families of birds represented in avian samples from 16 Utah archaeological sites.

Family	No. of Species		No. of Specimens		Percent of Specimens		Minimum No. of Individuals	
	Archaic	Fre-mont	Archaic	Fre-mont	Archaic	Fre-mont	Archaic	Fre-mont
Podicipedidae: Grebes	2	3	481	19	32.24	0.54	76	10
Pelecanidae: Pelicans	1	1	9	233	0.60	6.56	2	25
Phalacrocoracidae: Cormorants	1	1	1	21	0.07	0.59	1	4
Ardeidae: Herons, Bitterns	3	6	9	106	0.60	2.99	4	31
Plataleidae: Ibises, Spoonbills	—	1	—	1	—	0.03	—	1
Anatidae: Swans, Geese, Ducks	12	22	765	2582	51.27	72.71	107	504
Accipitridae: Hawks, Eagles, Harriers	4	4	19	48	1.27	1.35	8	26
Falconidae: Falcons	1	3	9	14	0.60	0.39	4	10
Tetraonidae: Grouse	4	4	48	239	3.22	6.73	13	37
Gruidae: Cranes	1	1	30	7	2.01	0.20	4	3
Rallidae: Rails, Gallinules, Coots	1	3	3	143	0.20	4.03	3	34
Charadriidae: Plovers, Turnstones	—	1	—	2	—	0.06	—	1
Scolopacidae: Snipe, Sandpipers	1	3	8	13	0.54	0.37	4	11
Recurvirostridae: Avocets, Stilts	1	2	5	27	0.34	0.76	2	10
Stercorariidae: Jaegers, Skuas	1	—	1	—	0.07	—	1	—
Laridae: Gulls, Terns	2	2	17	11	1.14	0.31	7	5
Columbidae: Pigeons, Doves	2	1	2	2	0.13	0.06	2	2
Strigidae: Owls	3	4	23	31	1.54	0.87	12	14
Picidae: Woodpeckers	1	1	3	1	0.20	0.03	3	1
Corvidae: Jays, Magpies, Crows	2	3	51	45	3.42	1.27	16	17
Icteridae: Meadowlarks, Blackbirds	1	3	3	6	0.20	0.17	3	5
Passeriformes: Family Indeterminate	2?	—	5	—	0.34	—	4	—
TOTALS	46	69	1492	3551	100.00	100.02	276	751

possible to separate these forms or races osteologically. Eight elements (3 to 4 individuals) from an extremely large race of *B. canadensis* (Linnaeus) compared closely with those of *B. c. maxima* (Injun Creek site). Seven other specimens of geese from this site and one from Unnamed site are probably *B. c. hutchinsii*. It is of interest to note that elements of the Snow Goose, *Chen caerulescens* (Linnaeus), were more numerous than those of the Canada Goose (441 versus 312); the former species is presently considered an uncommon transient in the state. Thirteen bones of Ross' Goose, *Chen rossii* (Cassin), reported by Hayward et al. (1976) as a casual although regular migrant through Utah, were identified from the Levee and Knoll sites.

Approximately 45 percent of all identified avian remains, representing a minimum of 17 species, were those of ducks. Identification problems involving duck elements have been discussed. Osteological similarities between species such as the Cinnamon Teal (*Anas cyanoptera* Vieillot) and Blue-winged Teal (*Anas discors* Linnaeus), Mallard (*Anas platyrhynchos* Linnaeus) and Black Duck (*Anas rubripes* Brewster), and Lesser Scaup (*Aythya affinis* (Eyton)) and Ring-necked Duck (*Aythya collaris* (Donovan)), to cite just a few examples, prompted the combination of some elements of certain closely related species under general categories (e.g., Mallard-Black Duck-Pintail group). None of the identified species of ducks is unusual with regard to current abundance or distribution in the Great Salt Lake and Bear River Refuge marshes.

Family Accipitridae—Hawks, Eagles, and Harriers

Raptors belonging to this family were poorly represented. Although remains of at least five species were identified, the number of hawk and eagle elements accounted for less than 2 percent of the total sample. The significance of these birds to prehistoric aboriginal groups that once occupied this region is unknown, although ethnographic data indicate that raptorial birds were of considerable symbolic and ceremonial significance to historic groups (e.g., the Hopi: Fewkes 1900). Eagle trapping was a well established tradition among most tribes of the Great Plains as well as several others in the Southwest. During such hunts, where the birds were grabbed by hand by a concealed hunter when the hawk or eagle attempted to take strategically placed bait, numerous hawks and eagles were usually captured. In a study of approximately 3100 avian remains from 51 South Dakota Arikara sites, a total of nearly 1300 elements (around 43 percent) were identified as those of hawks and eagles (Parmalee 1977). Although several species of *Buteo* hawks, the Marsh Hawk, *Circus cyaneus* (Linnaeus), and the Golden Eagle, *Aquila chrysaetos* (Linnaeus), occur commonly over much of Utah, for whatever reason they appear to have rarely been captured by the prehistoric inhabitants of the area.

Family Falconidae—Falcons

Osteological similarities between the Prairie Falcon, *Falco mexicanus* Schlegel, and the Peregrine Falcon, *Falco peregrinus* Tunstall, often limit the ability reach accurate species determinations; incomplete elements further complicate the problem. For these reasons several elements of these falcons were recorded as *Falco* sp. (Table 2). Nine of the 21 falcon specimens compared most closely with *F. peregrinus*, yet only two could be identified as Prairie Falcon. Behle and Perry (1975:15) list the Prairie Falcon as a common permanent resident in Utah today, and the Peregrine Falcon as "formerly a permanent resident . . . but present status essentially a rare transient." Hayward et al. (1976:67) comment that some of the early investigators in Utah considered the Peregrine Falcon to be "rather common." As was the case with representatives of the Accipitridae, few falcons were taken by aboriginals inhabiting these sites.

Family Tetraonidae—Grouse and Ptarmigan

Bones of four species of grouse made up approximately 6 percent of all identifiable avian remains. Specimens of grouse, not unlike the broken elements of ducks, often defy species determination. Although all four species are now considered by Behle and Perry (1975) as uncommon permanent residents in Utah, the Sharp-tailed Grouse, *Pedioecetes phasianellus* (Linnaeus), and Sage Grouse, *Centrocercus urophasianus* (Bonaparte), were formerly more widespread and abundant. Elements of grouse occurred in 11 of the 16 sites, but were most numerous in those sites such as Nephi and Pharo Village that were located in more open desert areas.

Family Gruidae—Cranes

Remains of the Sandhill Crane, *Grus canadensis* (Linnaeus), occurred in only three sites. The paucity of specimens is surprising since this bird was reported as formerly a common summer resident in northern Utah (Hayward et al. 1976:74). The distal end of a left humerus and proximal ulna of a Sandhill Crane had been cut from the shaft by the "groove-and-snap" technique (Parmalee 1976:152, Fig. 76); the shafts of major wing elements from large birds were often modified for the manufacture of whistles and other bone tube instruments. Except for an incomplete coracoid from Deadman Cave that is referable to the Little Brown Crane, *Grus c. canadensis,* all other elements were from birds of the large race, *G. c. tabida* (Peters).

Family Rallidae—Rails, Gallinules and Coots

Specimens of the American Coot, *Fulica americana* Gmelin, were the most numerous and occurred in 11 of the 16 sites. Only at the Levee site, however, can elements of this species be considered numerous (76 bones from a minimum of 11 individuals). In light of the summer abundance of this species at the Great Salt Lake and the relative ease with which it can be taken, 11 individuals appears to be a small number for such a potential food resource.

Behle and Sperry (1975) note only two verified records of the Purple Gallinule, *Porphyrula martinica* (Linnaeus), for Utah and consider its status as accidental. It is of interest, therefore, that two individuals of this species were identified on the basis of six elements (two incomplete humeri, paired distal ends of tibiotarsi, complete left femur, and coracoid) recovered at the Levee site.

Family Charadriidae—Plovers and Turnstones

A complete left tarsometatarsus and distal one-third of a tibiotarsus of the Black-bellied Plover, *Pluvialis squatarola* (Linnaeus), a common transient through Utah during spring and fall migrations, were the only elements recovered (Bear River No. 3) of species belonging to this family.

Family Scolopacidae—Snipe and Sandpipers

The rather large group of birds generally termed "shorebirds" appear to have been of little importance to prehistoric Indian groups inhabiting northern Utah. Although elements of four species, the Common Snipe (*Capella gallinago* (Linnaeus)), Long-billed Curlew (*Numenius americanus* Bechstein), Greater Yellowlegs (*Tringa melanoleucus* (Gmelin)), and the Willet (*Catoptrophorus semipalmatus* (Gmelin)), were identified from nine sites during this study, no more than three individuals were represented at any one site (Table 2). Behle and Perry (1975) state that the Long-billed Curlew was formerly a common summer resident and transient. In view of its large size and apparent availability, one might surmise that this species was a valuable supplemental food resource, but such was not the case.

Family Recurvirostridae—Avocets and Stilts

Both the American Avocet, *Recurvirostra americana* Gmelin, and Black-necked Stilt, *Himantopus mexicanus* (Müller), are considered by Behle and Perry (1975) as common summer residents in northern Utah and transient throughout the state. Remains of the American Avocet occurred at six sites and the maximum number of individuals represented at any one site (Levee) was five. Like species belonging to the Charadriidae and Scolopacidae, these birds were seldom or rarely taken by the Indian. The Black-necked Stilt was represented in the faunal samples by only a single element, a nearly complete right humerus from the Levee site.

Family Stercorariidae—Jaegers and Skuas

A complete left carpometacarpus, tentatively identified as a parasitic Jaeger, *Stercorarius parasiticus* (Linnaeus), occurred in the faunal sample from Black Rock II. This species is reported by Behle and Perry (1975) as an occasional visitor in late summer and early fall; the majority of specimens that have been observed or collected occurred in the vicinity of the Bear River Refuge.

Family Laridae—Gulls and Terns

Elements of gulls were recovered from eight sites. One species, the California Gull, *Larus californicus* Lawrence, was identified from four bones from Deadman Cave. A furculum and scapula of a gull (*Larus californicus*? or *L. delawarensis*? Ord) from Sandwich Shelter exhibited butchering cuts, indicating that the bird had been processed by the inhabitants. The Caspian Tern, *Hydroprogne caspia* (Pallas), an uncommon summer resident in northern Utah, was represented by a single element at Deadman Cave and the Knoll site. As a group, gulls and terns appear to have been of only minor importance; all elements combined amounted to less than 1 percent of the total.

Family Columbidae—Pigeons and Doves

Doves appear to have been of little or no value to the Indians who occupied northern Utah, judging by the paucity of their remains encountered at archaeological sites. Although the Mourning Dove, *Zenaidura macroura* (Linnaeus), is common throughout Utah during the summer months, it was represented by only three elements in the 16 faunal samples, two humeri from the Nephi site and one from Stansbury II. Hargrave (1970) reported a single humerus from the Sand Dune Cave collections. The recovery of a partial left humerus (missing distal end) of a Passenger Pigeon, *Ectopistes migratorius* (Linnaeus), from the Stansbury II site is especially noteworthy. Neither Behle and Perry (1975) nor Hayward et al. (1976) list the Passenger Pigeon as a former inhabitant of Utah. Although Schorger (1973: Fig. 22) provides casual or accidental records for several western states (Wyoming, Idaho, Montana, Nevada), there are none for Utah. The specimen from the Stansbury II site apparently represents the first record of Passenger Pigeon from the state.

Family Strigidae—Owls

As a group, owls were of special significance to a large number of aboriginal people in North America, not particularly as a food resource but as symbols of the supernatural, of strength and other desirable qualities, and of death and as group totems. Sperry (1957) lists owl feathers from Danger Cave, Hargrave (1970) records them from Sand Dune Cave, and elements of several species of owls have been reported from Hogup Cave (Parmalee 1970), Bear River No. 2 (Laybourne 1967), and other archaeological sites in Utah. Remains of at least four species of owls were encountered in 12 of the 16 avian samples examined during this study. The Great Horned Owl, *Bubo virginianus* (Gmelin), was the most numerous (28 pieces, a minimum of 11 individuals). Elements of the Short-eared Owl, *Asio flammeus* (Pontoppidan), and/or Long-eared Owl, *Asio otus* (Linnaeus), both common permanent residents in Utah, were also numerous (21 specimens representing 11 individuals). Of interest was the recovery of a nearly complete left femur of the Spotted Owl, *Strix occidentalis* (Xántus), from Pharo Village, a bird reported by Behle and Perry (1975) as being a rare permanent resident in Utah. Two elements of the Great Horned Owl exhibited butchering marks: the distal end of a humerus from Stansbury II (removal of the outer wing) and the shaft and intercotylar process of a tarsometatarsus (removal of the lower leg) from Sandwich Shelter. Removal of these outer limb elements suggests their possible use in ceremonial functions or as decorative items, as evidenced by finds of these bones as human burial accouterments in other regions (Parmalee 1967).

Family Picidae—Woodpecker

Only one species of woodpecker, the Common Flicker, *Colaptes auratus* (Linnaeus), was represented in the avifaunas from four of the 16 sites, and then only one element from each. One Common Flicker element was recovered from Hogup Cave (Parmalee 1970); Hargrave (1970) records six feathers of this bird from Sand Dune Cave and mentions a find of eight rectrices from Cave Dupont, Kane County, Utah, by Nusbaum (1922). The significance of woodpecker feathers for various forms of decoration and the use of "stuffed" skins (possibly as symbolic objects) has been demonstrated by the recovery of such remains from Lovelock Cave, Nevada (Loud and Harrington 1929) and other archaeological sites in the Southwest (Hargrave 1970). The incorporation of feathers, including those of woodpeckers, as decoration in Pomo basketry is well known (Barrett 1908). The paucity of osteological remains of woodpeckers from the sites studied suggests that they were of little importance to these people, although 10, or possibly 11 species of woodpeckers are known to occur in Utah (Behle and Perry 1975).

Family Corvidae—Jays, Magpies, and Crows

Although three species of corvids were represented in the samples, those of the Common Raven, *Corvus corax* Linnaeus, were the most numerous and occurred in 12 of the 16 sites. The raven was esteemed or considered by many aboriginal groups as a bird possessing certain supernatural powers or symbolic traits and consequently it often served as a clan totem. Feathers, various body parts, and whole skins were worn or carried. These artifacts, occasionally buried with their owner, have been encountered (skulls, wing and leg elements) as burial accouterments (Ubelaker and Wedel 1975). In a study of bird remains from Arikara sites in South Dakota, I reported that elements of corvids made up approximately 15 percent of the 3100 bones examined (Parmalee 1977); those of ravens amounted to 10 percent of the total. Clark's Nutcracker, *Nucifraga columbiana* (Wilson), and the Black-billed Magpie, *Pica pica* (Linnaeus), both common permanent residents throughout most of Utah, were represented by only six individuals. The paucity of remains of these two species and the total lack of Common Crow, *Corvus brachyrhynchos* Brehm, elements, a common winter visitant, suggests that the Common Raven was the only corvid of significance to these people.

Family Icteridae—Meadowlarks, Orioles, and Blackbirds

Remains of three species belonging to this family were identified from the avian samples, but the small number of bones recorded (nine pieces, eight individuals) suggests that, as a group, these birds were taken only occasionally. Whether they represent a minor food supplement in the diet or perhaps a source of decorative feathers is a matter of speculation. Hargrave (1970) reported finding pieces of skin and feathers (the red, buff, and black wing coverts) of an adult male Red-winged Blackbird, *Agelaius phoeniceus* (Linnaeus), at Sand Dune Cave.

Family Indeterminate

Five indeterminate passerine elements, two of which were incomplete right humeri of a small fringilid (?), were recovered at Sandwich Shelter. The significance of these, or any small passerine birds to aboriginal groups who once inhabited this region, is difficult to evaluate. The apparent scarcity of osteological remains in sites might imply a general disregard for these small birds, yet their poor representation in most avifaunas may also be attributed to archaeological field excavation/recovery techniques. Until fairly recent times, ¼-inch (approximately 0.64-cm) hardware cloth was used to screen the soil being removed during excavation, and elements of small vertebrates simply passed through such coarse screens and were lost. There are exceptions, of course, and one of the most notable is based on the analysis of feathers from Hogup Cave reported by Baldwin (1970). Of the 13 species of birds identified from feathers recovered at Hogup Cave, those of the Gray-crowned Rosy Finch, *Leucosticte tephrocotis* (Swainson), were the most numerous (58 percent of the total) and occurred in 15 of the 16 excavated strata.

The fact that various passerines were taken for their skins or plumage has been well documented in the ethnographic literature. The strip of skin and feathers of a Rufous-sided Towhee, *Pipilo erythrophthalmus* (Linnaeus), found as a "choker" at the neck of a human infant in a burial taken from the Catfish Canyon Site, Glen Canyon area (Hargrave 1960) provides an interesting example. However, unmodified remains of small birds recovered in cave site deposits, for example those of Horned Lark, *Eremophila alpestris* (Linnaeus), reported by Sperry (1957) from Danger Cave and others identified from Hogup Cave, may represent prey individuals taken by raptors, which also periodically use cave sites as roosts (Parmalee 1970).

SUMMARY AND CONCLUSIONS

In order to reach what might be considered an accurate interpretation of any archaeological faunal sample, the almost limitless number of variables that may have affected that sample—such as preservation factors, length of site occupation, number of occupants, season(s) of occupation, occupants' hunting methods and preferences for certain animals, percentage of the site sampled, and field recovery techniques—must be evaluated. Ethnographic accounts of hunting techniques and food preparation methods, for example the communal duck and coot hunt of the Shoshone described by Lowie (1924), can provide a useful correlation with the osteological record. However, the applicability of ethnographic data in interpreting prehistoric archaeological faunas may indeed be questionable. Therefore, interpretation of an osteological sample must take into account as many of the variables as might be considered applicable. In spite of the unknowns, the identification of species, the number of remains of each, and an estimate of the number of individuals represented can prove indicative of the relative importance of a species or group of animals in the social and/or economic life of a people.

The identification of approximately 5050 bird bones from 5 Archaic and 11 Fremont sites located in northern and western Utah has shown a relatively consistent utilization of some avian groups (e.g., geese and ducks) over several thousand years. In contrast, other species were apparently not consistently used. Grebe elements made up nearly 33 percent of all avian remains from the Archaic sites, but less than 1 percent of the Fremont samples. Bones of the White Pelican, on the other hand, totaled about 7 percent of the remains from the Fremont sites, but less than 1 percent from the Archaic. Although there were more than twice the number of elements from the Fremont sites, it is doubtful that this difference in sample size is a factor in explaining such discrepancies. Nor are differences in seasonal occupation of the sites: both the Eared Grebe and White Pelican are common summer residents and, therefore, would have been available to both cultural groups. Perhaps hunting methods or a preference for other species were factors affecting the taking of one species and not another.

All of the species represented in the 16 archaeological samples, except the Passenger Pigeon, either still occur in Utah or represent birds previously reported from the state. Thirteen of the 16 sites were located along or near the Great Salt Lake and Bear River marshes. As one might expect, remains of aquatic and semi-aquatic birds made up the majority of elements (approximately 90 percent in both Archaic and Fremont samples). When concentrations of waterfowl occurred on the Great Salt Lake, its marshes, and the rivers draining into it, the aboriginal peoples occupying these areas realized a valuable food resource that could be harvested with minimum effort for maximum return. The Indian had to be an opportunist in obtaining food; although preference was certainly a factor, abundance and availability of any given species or group of animals would have affected his procurement efforts as would a sufficient return for the amount of energy expended.

Elements of fledgling or juvenile birds were, as a whole, rare in the avian samples. Two young Ravens were represented in the material from Deadman Cave and several immature duck bones occurred in the Levee site sample. The largest number of elements of juvenile birds (15) were recovered at the Evans Mound site and included bones of Sage Grouse, Coot, hawk (*Buteo* sp.?), and Raven. This indicates a late spring/early summer occupation of this site. Osteological evidence from some aboriginal sites, for example the Emeryville Shellmound, San Francisco Bay, California, has shown that the inhabitants purposely hunted nestling birds, in this instance, cormorants (Howard 1929). In addition to the "groove-and-snap" Sandhill Crane wing bone ends described from Pharo Village, two others removed by the same method (distal right ulna of Bald Eagle, *Haliaeetus leucocephalus* (Linnaeus); proximal end of a right ulna of a Great Horned Owl) were found in the Deadman Cave material. Three limb bone shafts (goose humerus and tibiotarsus, eagle ulna) from which the ends had been removed were recovered at the Injun Creek site. These and other examples of scored or otherwise modified elements, special utilization of feathers and skins, and the interment of body parts with the dead are evidence that birds played an important role, in addition to subsistence, in the social and ceremonial activities of prehistoric Utah inhabitants.

ACKNOWLEDGMENTS

I express my appreciation to Jesse D. Jennings for the loan of the avian materials examined during this study; and to him and his Research Assistant, Frank Hull, I also owe a debt of gratitude for their patience in supplying site information and other pertinent data as well as reference materials. Examination of several of the faunal samples was initiated in 1972 when I was associated with the Illinois State Museum, Springfield; during this time the late Alexander Wetmore generously provided species determinations for several problem elements. I am also indebted to Amadeo M. Rea for identification assistance with certain bones and for the loan of comparative specimens.

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A FOSSIL PLAIN WANDERER (AVES: PEDIONOMIDAE) FROM FIRE-HOLE DEPOSITS, MORWELL, SOUTHEASTERN VICTORIA, AUSTRALIA

By Pat Vickers Rich[1] and A.R. McEvey[2]

ABSTRACT: Lacustrine deposits previously thought to be of mid-Miocene age from the Morwell open cut mine, southeastern Victoria, Australia, have produced the partial skeleton of a Plain Wanderer (Aves: Pedionomidae) indistinguishable from the living *Pedionomus torquatus* Gould. This indicates either a very young age for the Morwell Fire-hole No. 2 sediments (contrary to the mid-Miocene dating based on pollen analysis) or a very slow rate of evolution within the Pedionomidae. The former hypothesis is favored.

Lacustrine sediments of disputed age from Fire-hole No. 2, State Electricity Commission Open Cut Coal Mine at Morwell, Victoria (Australia) have produced a partial skeleton of a Plain Wanderer (Aves: Pedionomidae) indistinguishable from the living *Pedionomus torquatus*.

Both avian and marsupial skeletons were contained in finely laminated dark grey clays that formed a lenticular body, probably the remains of a small pond or lake. The depression in which deposition took place apparently formed when the early Miocene (Douglas and Ferguson 1976) brown coal of the Morwell Formation (Morwell 1A Seam) caught fire and burned in a restricted area. This steep-sided basin must have filled with water and served as a natural trap for animals that chanced to fall in, possibly, in the case of the kangaroos, through a vegetal mat that may have covered part of the pond's perimeter (T. Rich pers. comm.).

Analysis of the pollen (including *Triporopollenites bellus*) collected from these lacustrine sediments suggests a middle to late Miocene age (A. Partridge, ESSO, Sydney; pers. comm.), distinctly younger than the Morwell Formation, also palynologically dated. The marsupial fossils, on the other hand, including two species of kangaroos (*Macropus titan* (=*giganteus*) and *Protemnodon anak*; T. Rich and T. Flannery pers. comm.), are typical of Pleistocene-aged assemblages. *Macropus titan* might possibly extend into the Pliocene of western Victoria (Buninyong; T. Rich pers. comm.), but this would be the maximum age documented for this species. The following paper evaluates the partial skeleton of the Plain Wanderer from Morwell in light of this conflicting evidence.

Abbreviations used below are as follows: NMV, National Museum of Victoria, Melbourne; SAM, South Australian Museum, Adelaide.

SYSTEMATICS

Order Ralliformes (Reichenbach)

Family Pedionomidae Gadow

DIAGNOSIS: The Morwell fossil bird was assigned to the Pedionomidae because it exhibits the following combination of characters: *Sternum* with (1) a single sternal notch either side of the midline that extends about half the length of this element; (2) straight posterior lateral processes of equal width over their entire length.

Synsacrum with (1) foramina between vertebrae not well developed; (2) morphology broad, flat and not elongate, only slightly longer than wide; (3) anterior iliac crest, particularly near anterior end, prominent and separate from anterior blade of ilium, although the two nearly meet; (4) sacral vertebrae broadly expanded in comparison to remainder of vertebrae associated with synsacrum; (5) small anti-trochanter; (6) three or four vertebrae fused into synsacral complex posterior to sacrals (i.e., the synsacral caudals); (7) illioischiatic fenestra forming a small oval, not greatly elongate, but decidedly larger (at least three times the area) than acetabulum; (8) in ventral view only four parapophyses attaching to ilium anterior to sacral vertebrae, including one pair on anteromost vertebra, which is not completely fused into synsacral complex; (9) only one sacral parapophysis quite prominent, attaching onto ventral part of vertebral column; (10) no narrow ridge or distinct haemal processes on ventral parts of synsacral thoracic vertebrae; (11) most prominent pair of parapophyses of sacral vertebrae forming large acute angle with vertebral column instead of right angle.

Ulna (1) elongate and slender; with (2) shaft curved, not straight, particularly at proximal end; (3) shaft not distinctly compressed, but triangular in cross section with rounded edges, particularly at midpoint; (4) secondary papillae not prominent; (5) olecranon small and short, not prominent with palmar borders of internal and external cotyla not existing far

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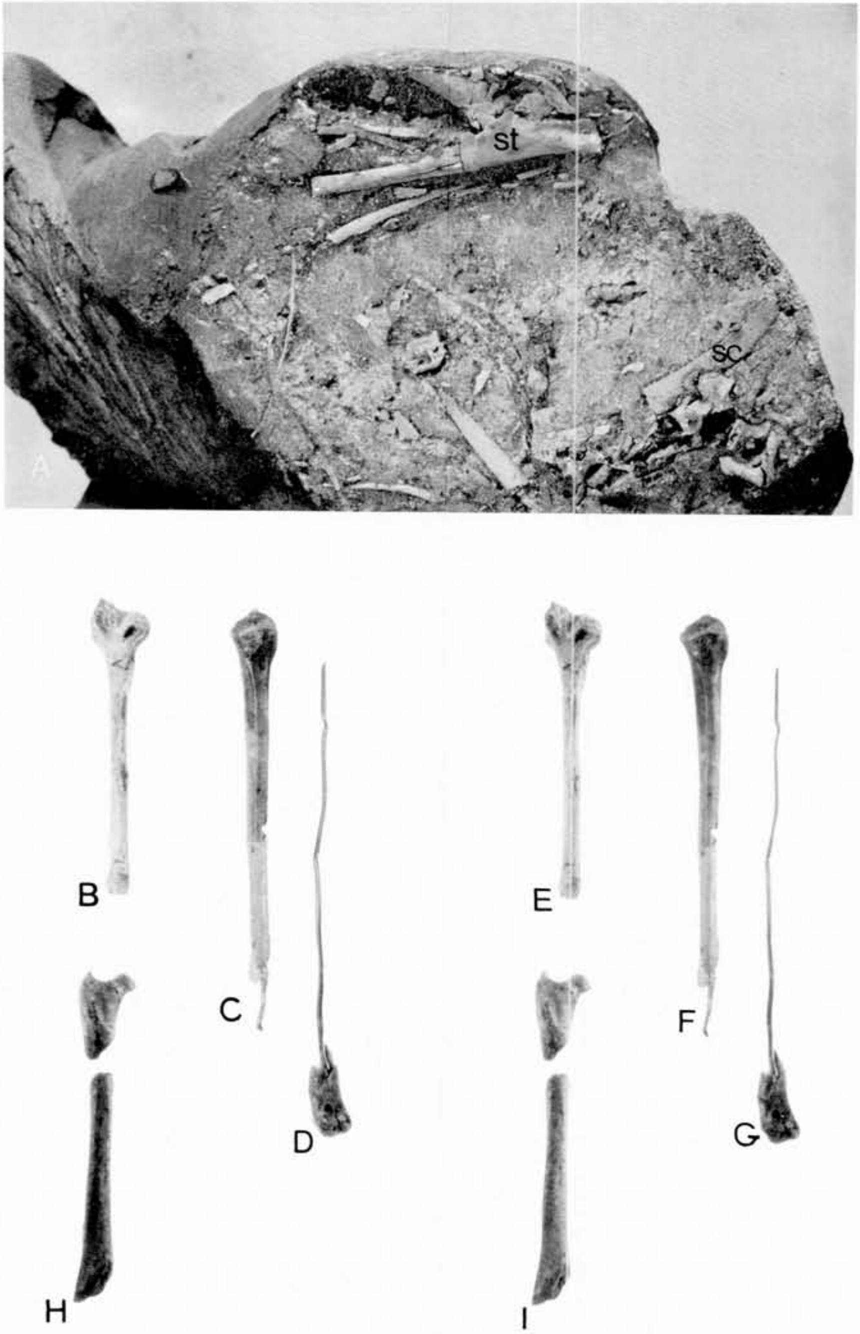

Figure 1. *Pedionomus torquatus* (NMV P39121), Fire-hole deposits, Morwell, Victoria: A partial skeleton in matrix including sternum (st), scapula (sc), and fragments of vertebrae and ribs. Stereographic pairs: B, E, tibiotarsus (lateral view); C, F, ulna (proximal fragments, palmar view); D, G, ulna (distal fragment, anconal view); I, H, femur (anterior view). See Table 1 for scale.

palmad of shaft; (6) distinct proximal radial depression absent, as is any great pneumatization in this area; (7) shaft surface near proximal end low and rounded palmarly, with only slight indication of median ridge; (8) prominence for anterior articular ligament low, not pronounced; (9) carpal tuberosity not prominent; (10) carpal tuberosity merging with shaft at about level where external condyle originates; (11) lateral margin of external condyle nearly parallel with lateral margin of shaft.

Femur with (1) trochanter well developed, deep; (2) proximal end not wide, but laterally compressed; (3) anterior and posterior borders of proximal end concave in proximal view, not straight and/or parallel; (4) proximal margin of trochanter, especially posterior half, recurved and overhanging iliac facet; (5) trochanter protruding anteriad of head; (6) trochanter slightly convex laterally, not highly convex, in proximal view; (7) trochanter not expanding much beyond anterior margin of shaft, lying nearly parallel to shaft in anterior or posterior views; (8) trochanter rising to marked peak, in lateral view, rather than being smoothly rounded; (9) trochanter extending farthest proximad just slightly anterior of its midpoint, in lat-

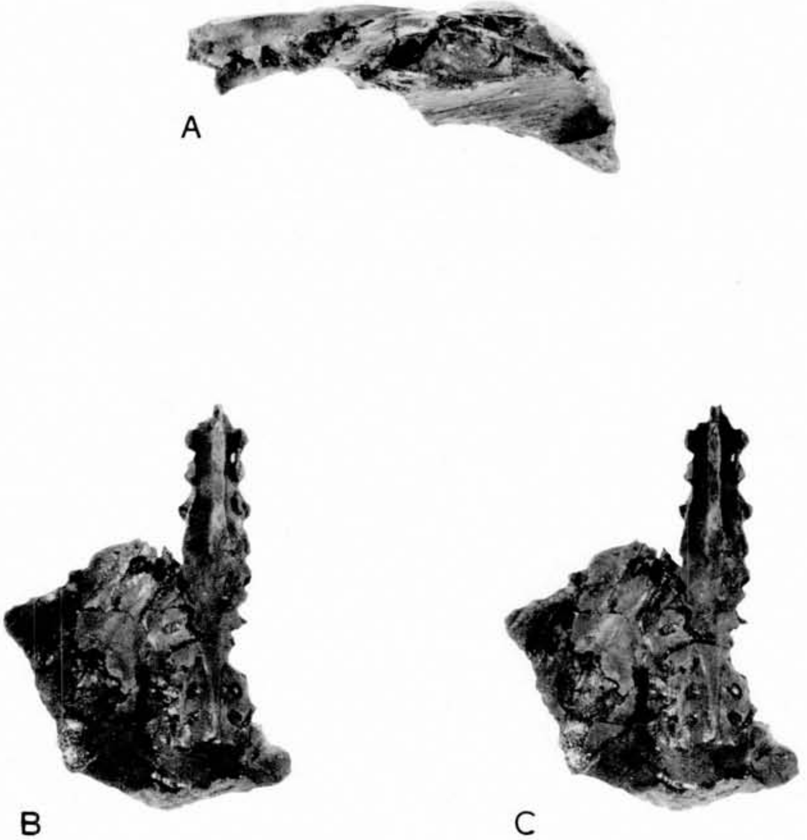

Figure 2. *Pedionomous torquatus* (NMV P39121), Fire-hole deposits, Morwell, Victoria: A, left lateral view of synsacrum; B, C, stereographic pair, dorsal view, synsacrum. See Table 1 for scale.

eral view; (10) iliac facet and head highly concave proximally, not flat; (11) proximal end lacking any projection anteriad along margin between trochanter and head; (12) shaft lacking deep excavation just internal to trochanteric ridge; (13) shaft lacking pneumatization on proximal end.

Tibiotarsus poorly preserved; (1) shaft compressed anteroposteriorly; (2) cnemial crests and rotular crests of moderate proximal extension; (3) interarticular area between external articular surface and rotular crest with relatively deep excavation; although there are no characters that exclude it from the Pedionomidae, the tibiotarsus has few diagnostic characters.

Genus *Pedionomus* Gadow

GENERIC DIAGNOSIS: As for family, only genus in family.

Pedionomus torquatus Gould

MATERIAL: NMV P39121, partial skeleton including: partial sternum (left half), ribs, distal fragments of left scapula, vertebral fragments, fused synsacral vertebrae, synsacral fragments, proximal end of right ulna, proximal end of left femur and midsection of left femur (not articulated), proximal end of left tibiotarsus (see Figs. 1–2). Found by Thomas Darragh. For measurements see Table 1.

LOCALITY: Fire-hole No. 2, State Electricity Commission Morwell Open Cut Coal Mine, Southeastern Victoria.

STRATIGRAPHIC HORIZON: Lacustrine sediments overlying Morwell Seam 1A (early Miocene) and below the Haunted Hill Gravels (Jenkin 1968). Age uncertain, lying between early Miocene and the pre-late Pleistocene.

DESCRIPTION AND COMPARISON: Sternum: Sternal notch slightly deeper, or posterior lateral process more elongate, or possibly both, than in *P. torquatus*; posterior lateral processes elongate and narrow with nearly straight lateral margin; intermuscular line prominent (variable in modern *Pedionomus*).

Scapula: Elongate, narrow, and parallel-sided over much of its length; of same size as in *P. torquatus,* except more robust, especially at the distal end.

Synsacrum: Two pairs of transverse processes anterior to main sacral vertebral attachment to synsacrum present in ventral view; prominent groove present along ventral midline between last lumbar and first sacral transverse processes; median dorsal ridge quite prominent; ventral border of synsacrum nearly straight in lateral view, not concave ventrally; synsacrum deepest at anterior end, narrowing posteriorly; arrangement of obturator foramen, acetabulum and ilio-ischiatic fenestrae as in *P. torquatus,* with the latter largest and ovoid in shape; synsacrum broad posterior to acetabulum as in Recent *P. torquatus*.

Table 1. Measurements (in mm) of Recent and fossil Pedionomidae.

Measurements	*Pedionomus torquatus* Morwell Victoria NMV P39121	Recent *Pedionomus torquatus* (n = 2)
STERNUM		
Length of sternal notch measured along internal side of left posterior lateral process	10.8+	9.6–11.2
Anterior width of posterior lateral process	~2.8	2.8–3.5
SYNSACRUM		
Total length of vertebral component of synsacrum, measured along dorsal surface	6.6	6.3–6.5
Maximum width across vertebral column just posterior to transverse process of first sacral vertebra	4.2	4.2–4.7
Diameter of right acetabulum	~2.4	1.8–1.9
Maximum measurement across right ilioischiatic fenestra	~4.6	5.1–5.5
Maximum measurement across right obturator foramen	~1.2	1.6–1.7
ULNA		
Proximal width	4.2	3.6–3.9
Proximal depth	2.9	2.0–2.9
Length from proximal end of olecranon to distal end of proximal radial depression	4.2	4.6–4.7
Depth of external condyle	2.4+	2.4–2.7
Distal width	3.4	3.1
FEMUR		
Proximal width	4.5	4.4–4.6
Depth of trochanter	3.2	3.1–4.1
Depth of head	1.9	2.0
TIBIOTARSUS		
Distance from external articular surface to distal end of fibular crest	10.8	9.2–9.4
Depth across external articular surface to base of external cnemial crest	4.1	3.9–4.1
Width of shaft at base of fibular crest	2.5	2.4
Depth of shaft at base of fibular crest	1.6	1.5–2.5

Ulna: No appreciable differences from *P. torquatus,* although distal end fragmentary.

Femur: Although differences exist between the proximal ends of some femora of Recent *P. torquatus* and the Morwell specimen, it lies within the range of variability found in living *P. torquatus*; the shaft shape compares closely with that of the living species, the only visible difference being a slightly greater anteroposterior flexure in lateral view, being convex anteriorly rather than straight; direct connection between the proximal and distal segments of the femur cannot be established, but the two fragments are very probably from the same bone.

Tibiotarsus: Comparison very limited because of erosion of proximal end, but appears similar to *P. torquatus*. See Bock and McEvey (1969) for a thorough, complete description of the skeleton of the living *P. torquatus*.

In summary, then, the Morwell *Pedionomus* is the same size as the living *P. torquatus* and differs only in that (1) the sternal notch is slightly deeper, (2) the ventral border of the synsacrum is not as curved (concave ventrally), and (3) the shaft of the femur may have a slightly greater flexure. Because our sample of living *P. torquatus* is so small and the differences noted above only slight, we believe there is no reason to propose a new species for the fossil material. The reasoning is strengthened by the fact that several skeletal elements are represented, and all show only minor differences, if any, from *P. torquatus*.

DISCUSSION AND CONCLUSIONS

Detailed comparisons of several skeletal elements of the fossil Plain Wanderer from Morwell with those of Recent *Pedionomus torquatus* show few differences, either qualitative or quantitative. The differences noted are insufficient to define a new species. The close similarity between the fossil specimen and Recent *P. torquatus* suggests two possibilities. The first is that the lacustrine sediments at Morwell are very young. This is because within avian groups with known lengthy records in Australia, such as the Aegothelidae (Rich and McEvey 1977) and Phoenicopteridae (Miller 1963), pre-Pleistocene forms show significant differences from extant birds. This is also true in areas where the record of fossil birds is far better

(Wright et al. 1973; Harris 1977; Van Devender et al. 1977; Porter 1978; Van Devender and Spaulding 1979), and these periods may have seen the extensive development of forests and open woodlands. However, it is unlikely that the archaeological records represent relict, post-Pleistocene populations of *E. migratorius* that resulted from climatic changes and their effect on vegetation patterns. It is more likely that Holocene climatic fluctuations, causing minor mesic intervals, allowed *E. migratorius* to re-extend its range into the state. Pollen studies have shown increases in moisture at Picuris Pueblo from A.D. 1335–1425 (Schoenwetter 1970) and at Chaco Canyon beginning about A.D. 1100 (Hall 1977). These periods may represent brief mesic intervals that allowed *E. migratorius* to expand into those areas.

CONCLUSIONS

Two new records of *Ectopistes migratorius* are the earliest Holocene records known from New Mexico. Pleistocene records of this species indicate that it was possibly common in the state at that time. It is questionable, however, that it was able to remain in New Mexico as relict populations following post-Pleistocene climatic changes. Rather, it probably re-extended its range into certain areas because of temporary climatic fluctuations that caused minor mesic intervals. We expect there will be other Pleistocene and archaeological records of *E. migratorius* in the western United States.

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PASSENGER PIGEON BONES FROM ARCHAEOLOGICAL SITES IN NEW MEXICO

By L.L. Hargrave[1] and S.D. Emslie[2]

ABSTRACT: Three bones of the Passenger Pigeon, *Ectopistes migratorius* (Linnaeus), were recovered from archaeological sites in Taos and San Juan Counties, New Mexico. The elements represent at least two individuals and could date as early as A.D. 975. These records are the first Holocene records of *E. migratorius* in New Mexico and increase this species' known distribution in prehistoric western United States.

The extinct Passenger Pigeon, *Ectopistes migratorius* (Linnaeus), was a species whose preferred habitat was the forested areas of eastern North America (Ridgway 1916; Schorger 1955). There are only a few known records of this pigeon from western states; these include Idaho (Burleigh 1972), Nevada (Linsdale 1951), Washington (Jewett et al. 1953), and Wyoming (Ridgway 1916).

Howard (1937) described six elements representing at least two individuals of *Ectopistes migratorius* from the late Pleistocene deposits of Rancho La Brea. These specimens represented the first record of the Passenger Pigeon from California, and the first fossil record of this species from the western United States. A second fossil record from the western United States, also reported by Howard (1971), consisted of one bone from Pleistocene deposits in Dark Canyon Cave, Eddy County, New Mexico. Regarding the date of deposits in this cave, Howard (pers. comm.) states, "The Avifauna from Dark Canyon Cave certainly suggests a Late Pleistocene date of deposition. The three best represented species are *Coragyps occidentalis* (Miller), *Gymnogyps amplus* Miller, and *Caracara prelutosa* (Howard), which are characteristic of the Rancho La Brea avifauna, and have been found at other Late Pleistocene localities in the United States and Mexico."

MATERIAL

The specimens of *Ectopistes migratorius* reported on here were recovered from the archaeological sites of Una Vida in Chaco Canyon, San Juan County, and Picuris Pueblo (San Lorenzo), Taos County (Fig. 1). The specimens are:

Una Vida: right humerus complete, No. C265 (length: 43.0 mm), Room 46, floor. Left ulna with proximal end fragmented, No. C271 (approximate length: 47.3 mm), Room 65.

Picuris Pueblo: left tibiotarsus with the ends fragmented, No. 1192, TA III, Area III Test Pit C, bottom layer.

The Passenger Pigeon bone from Picuris Pueblo is currently housed at Adams State College, Alamosa, Colorado 81102 (in the care of Herbert Dick); the two bones from Una Vida are housed at the Chaco Center, University of New Mexico, P.O. Box 26176, Albuquerque, New Mexico 87125 (in the care of James Judge).

Una Vida is a large classic Chaco town of the Anasazi culture, Rooms 46 and 65 are contemporaneous and were dated by tree rings, architectural style, and ceramic typology to within the period A.D. 950–1030, with a more probable range of A.D. 975–1030 (Gordon Vivian pers. comm.). Picuris Pueblo has been continuously occupied since A.D. 1250. Ceramic evidence indicates the provenience in which the bone was found dates at A.D. 1300–1350 (Herbert Dick pers. comm.).

IDENTIFICATION

Pigeons other than *Ectopistes migratorius* whose remains might occur in archaeological sites in the western United States include the Band-tailed Pigeon, *Columba fasciata* Say, the Red-billed Pigeon, *C. flavirostris* Wagler, and the domestic Rock Dove, *C. livia* Gmelin. The latter species was introduced into North America but may occur intrusively in a prehistoric site and is especially important to consider here as Picuris Pueblo is also a historic site that is still inhabited. In addition, Hargrave identified bones of the Band-tailed Pigeon at Picuris Pueblo.

Comparisons were made with 26 adult skeletons of *Ectopistes migratorius,* 17 of *Columba fasciata,* 20 of *C. livia,* and six of *C. flavirostris.* Five skeletons of the White-crowned Pigeon, *C. leucocephala* Linnaeus, were also included in the comparisons. *E. migratorius* is distinguished from the species of *Columba* by having humerus with stockier shaft; deltoid crest more rounded, ectepicondylar papilla higher on shaft; and external condyle more elongate.

Ulna with a small depression on proximal intercotylar ridge (this depression is absent in *Columba flavirostris* and there is a small projection on the ridge in *C. leucocephala*); and bicipital attachment placed closer to impression of M. brachialis anticus.

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known, especially in North America and Europe. The second possibility is an extremely slow rate of evolution within the Pedionomidae in comparison with other avian groups. No living species of bird anywhere in the world is known to extend farther back in time than the late Pliocene, approximately three million years ago.

In summary, we favor the hypothesis that the fossil Plain Wanderer from Morwell is of a late Pliocene or younger age. The presence of the fossil pedionomid is, likewise, suggestive of nearby grasslands during the time of deposition of the Firehole sediments as this is the ecological zone occupied by the living *P. torquatus*.

Pedionomus torquatus (SAM P126718) has previously been reported from Pleistocene deposits of Victoria Cave in South Australia (van Tets and Smith 1974). Although this synsacral fragment is similar to *P. torquatus,* it is likewise similar to several species of Charadriiformes. It differs from *P. torquatus* in having a narrow, prominent ridge on the ventral surface of the two anterior synsacral thoracic vertebrae and in being slightly more concave ventrally over the posterior half of the synsacral vertebrae. We hesitate to assign it to any taxonomic group until more material is available, because the specimen lacks so many of the characters diagnostic for the Pedionomidae.

ACKNOWLEDGMENTS

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ILLUSTRATIONS FROM "THE AVIFAUNA OF EMERYVILLE SHELLMOUND"

by HILDEGARDE HOWARD

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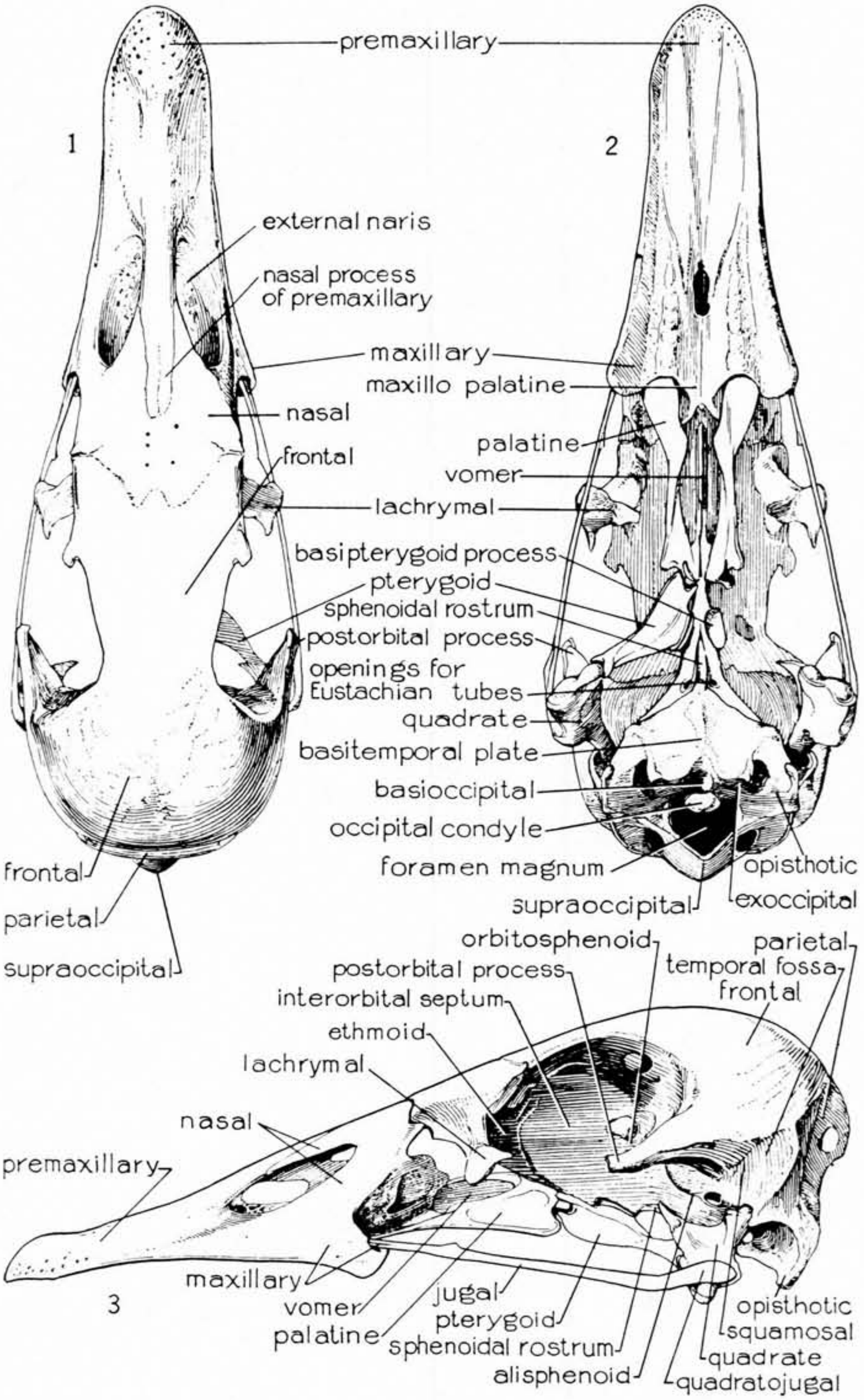
ILLUSTRATIONS OF AVIAN OSTEOLOGY TAKEN FROM "THE AVIFAUNA OF EMERYVILLE SHELLMOUND"

Of the many significant and invaluable contributions Hildegarde Howard has made to the field of avian paleontology, her paper entitled "The Avifauna of the Emeryville Shellmound" was one of the most important. This paper was published in 1929, and is especially cherished by those fortunate enough to obtain a copy. This work was not only a particularly valuable early contribution to avian paleontology, it contained a series of illustrations of the major bones of the avian skeleton with the major diagnostic features of each bone indicated and named. Over the past 50 years, these illustrations have proven very valuable, especially to new students of avian osteology. To this day they have not been surpassed for their usefulness as the terminology used in current studies of avian osteology remains based on that introduced by Dr. Howard. And anyone who has tried to orient a bone to determine view designations without the help of a mounted skeleton has often had cause to give thanks for the illustrations. That such a work remains so important after a period of 50 years testifies to its thoroughness and accuracy, two characters that have typified Dr. Howard's works through the years.

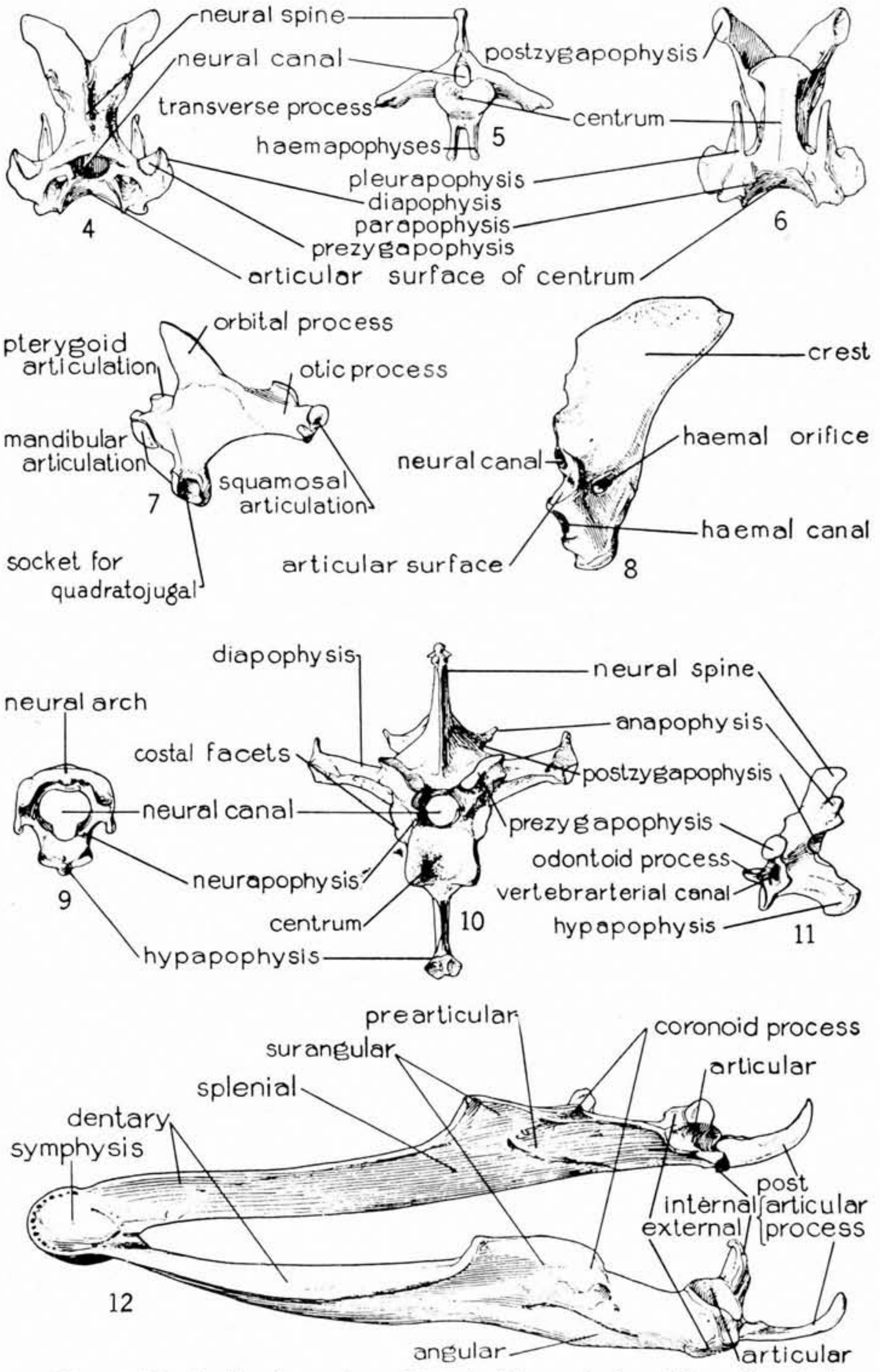
Even after 50 years Dr. Howard continues to receive many requests for copies of the Emeryville Shellmound paper; it is perhaps her most sought-after paper. For this reason we reproduce here the illustrations of avian osteological features from that paper. When speaking of the illustrations, Dr. Howard always credits William H. Burt for working with her in devising the nomenclatural system used in the illustrations, and Frieda Abernathy for executing the drawings. Quoted below are the explanatory notes for the illustrations, taken from page 325 of "The Avifauna of Emeryville Shellmound," by Hildegarde Howard, 1929, Univ. of California Publ. Zool. 32(2):301–394:

> Description of Species
>
> The terms employed in describing the diagnostic characters of the various represented species will be found in the accompanying series of labeled figures, drawn by Mrs. Frieda Abernathy.
>
> The system of nomenclature here set forth was devised by the writer in collaboration with Mr. William H. Burt, of the University of California. Papers by the following authorities were consulted: Furbringer (1888), Heilmann (1926), Lambrecht (1914), Lowe (1928), Miller (1925a, 1925b, 1927a), Milne-Edwards (1867–68), Owen (1866), Shufeldt (1890, 1909), Stresemann (1927), and Wetmore (1922, 1923). Dr. Miller and Dr. Wetmore were also consulted personally.
>
> The Golden Eagle (*Aquila chrysaetos*) and the Snow Goose (*Chen hyperboreus*) have been used for illustration. Such parts as cannot well be shown on *Aquila* are labeled on *Chen,* and vice versa. Of the Golden Eagle, Museum of Vertebrate Zoology specimen no. 28884 has been used except for figures 5 and 8, where MVZ no. 40866 was substituted; of the Snow Goose, MVZ no. 45555 has been drawn, except in figure 12 where MVZ no. 22446 has been used.

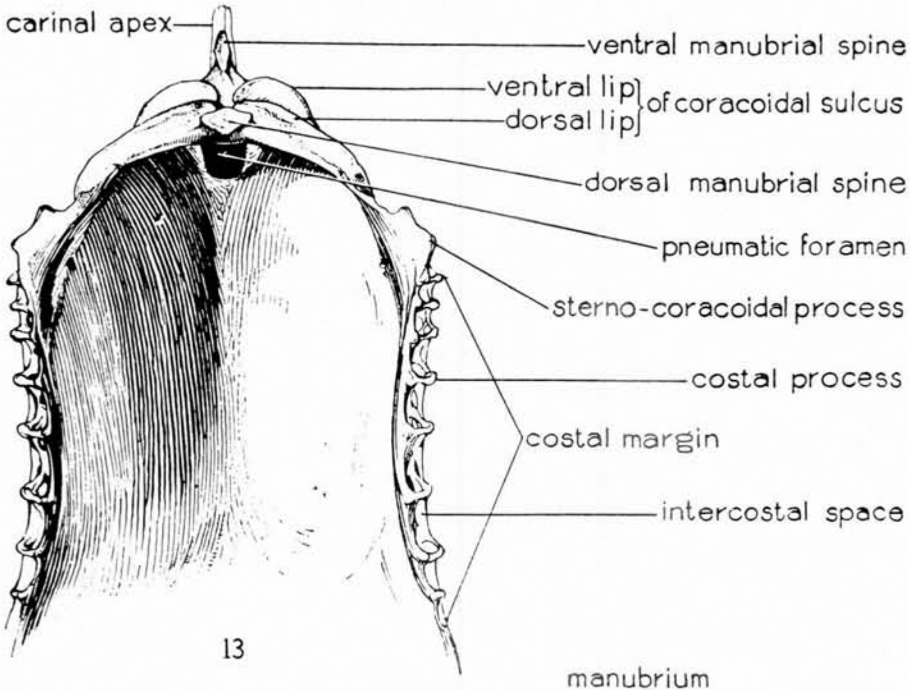
Grateful acknowledgment for permission to reprint the illustrations is given the University of California Press. Larry Reynolds provided unblemished photographs of the illustrations for reproduction here from a very well-worn copy of the original publication.



Skull of *Chen hyperboreus*. Fig. 1, dorsal view; fig. 2, ventral view; fig. 3, lateral view. × 1.



Figs. 4–11, *Aquila chrysaetos.* Fig. 4, 6th cervical vertebra, dorsal view; fig. 5, caudal vertebra, anterior view; fig. 6, 6th cervical vertebra, ventral view; fig. 7, left quadrate, external view; fig. 8, pygostyle; fig. 9, atlas, posterior view; fig. 10, 4th thoracic vertebra, anterior view; fig. 11, axis, left side; fig. 12, *Chen hyperboreus,* mandible. × 1.



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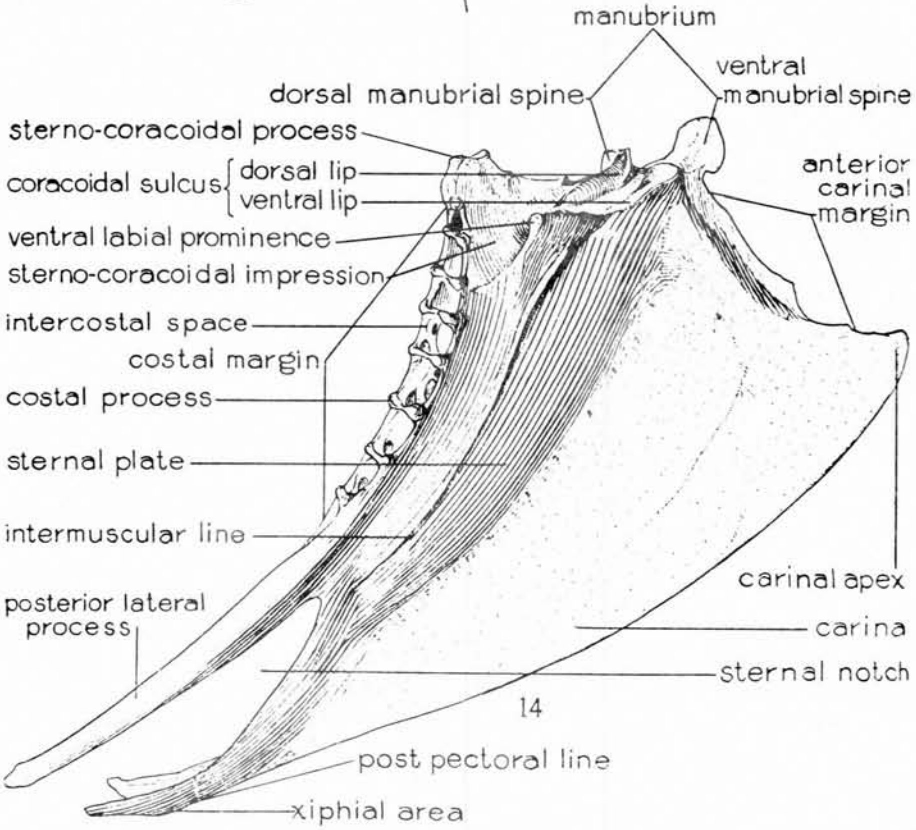

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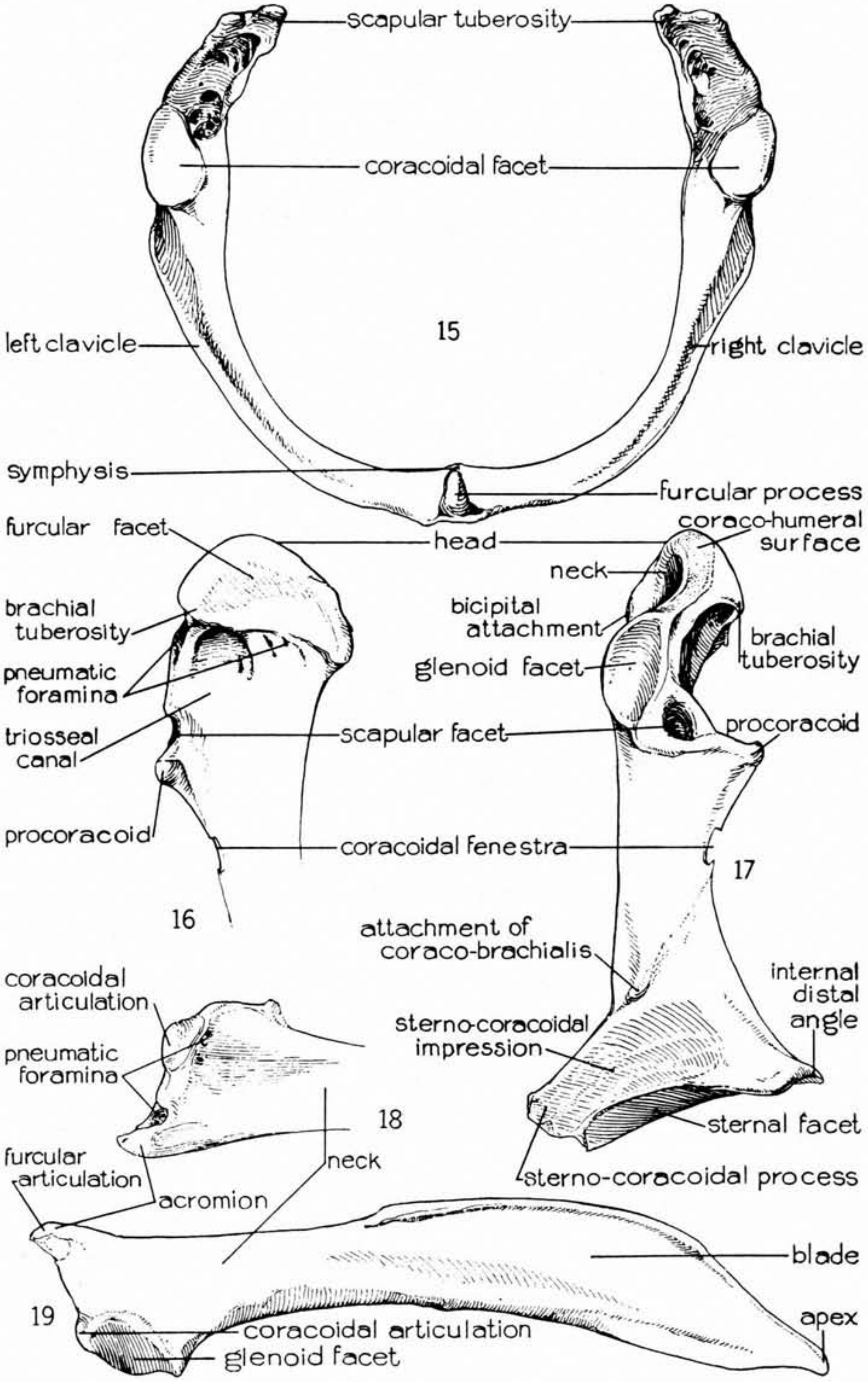
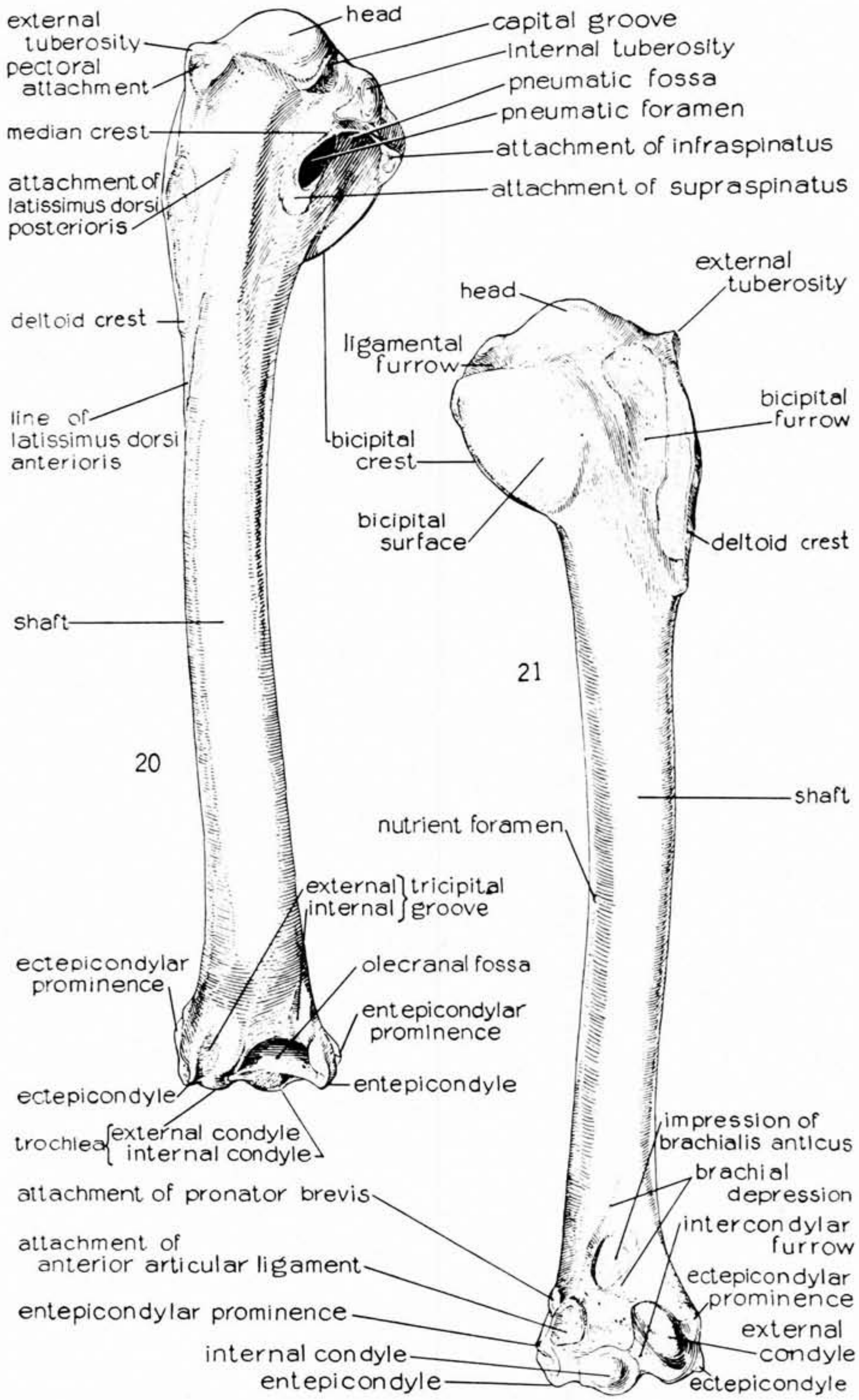
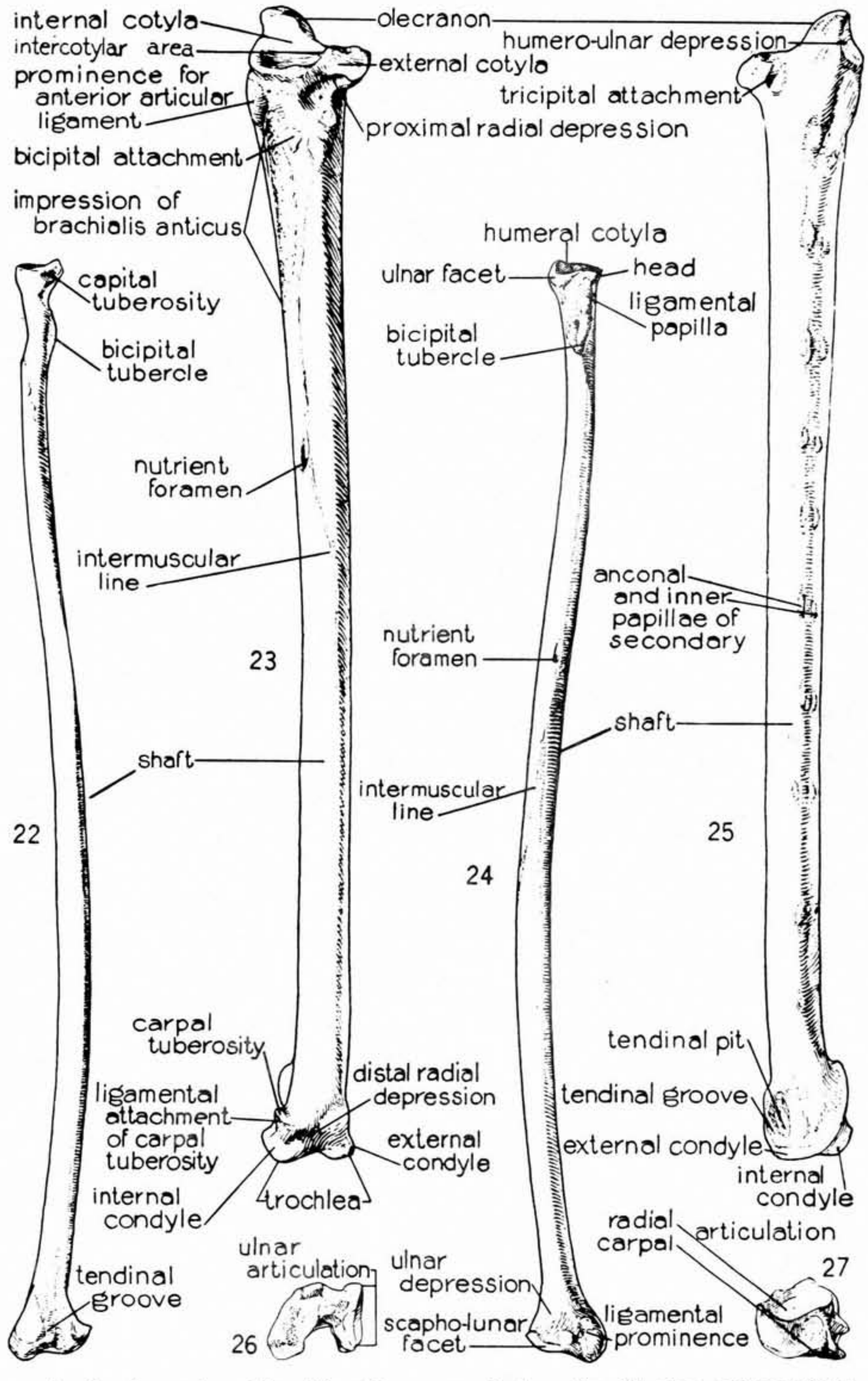
Sternum of *Chen hyperboreus*. Fig. 13, dorsal view; fig. 14, lateral view. × 1.



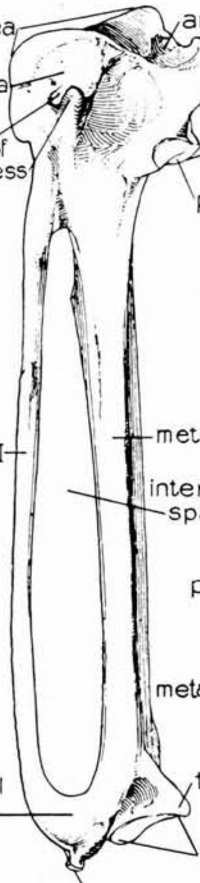
Aquila chrysaetos. **Fig.** 15, furcula, dorsal view; **fig.** 16, coracoid, internal view; **fig.** 17, coracoid, dorsal view; **fig.** 18, scapula, ventral view; **fig.** 19, scapula, dorsal view. × 1.



Humerus of *Chen hyperboreus*. Fig. 20, anconal view; fig. 21, palmar view. × 1.



Aquila chrysaetos. **Fig.** 22, **radius, anconal view; fig.** 23, **ulna, palmar view; fig.** 24, **radius, palmar view; fig.** 25, **ulna, anconal view; fig.** 26, **cuneiform; fig.** 27, **scapholunar. Figs.** 22–25 × 2/3; **figs.** 26–27 × 1.



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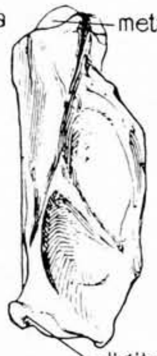

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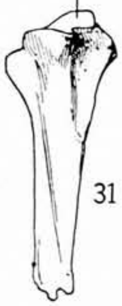

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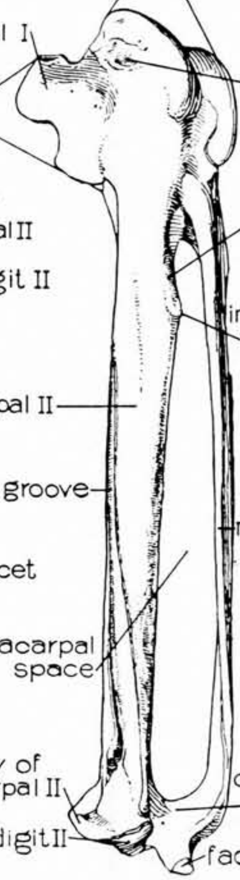

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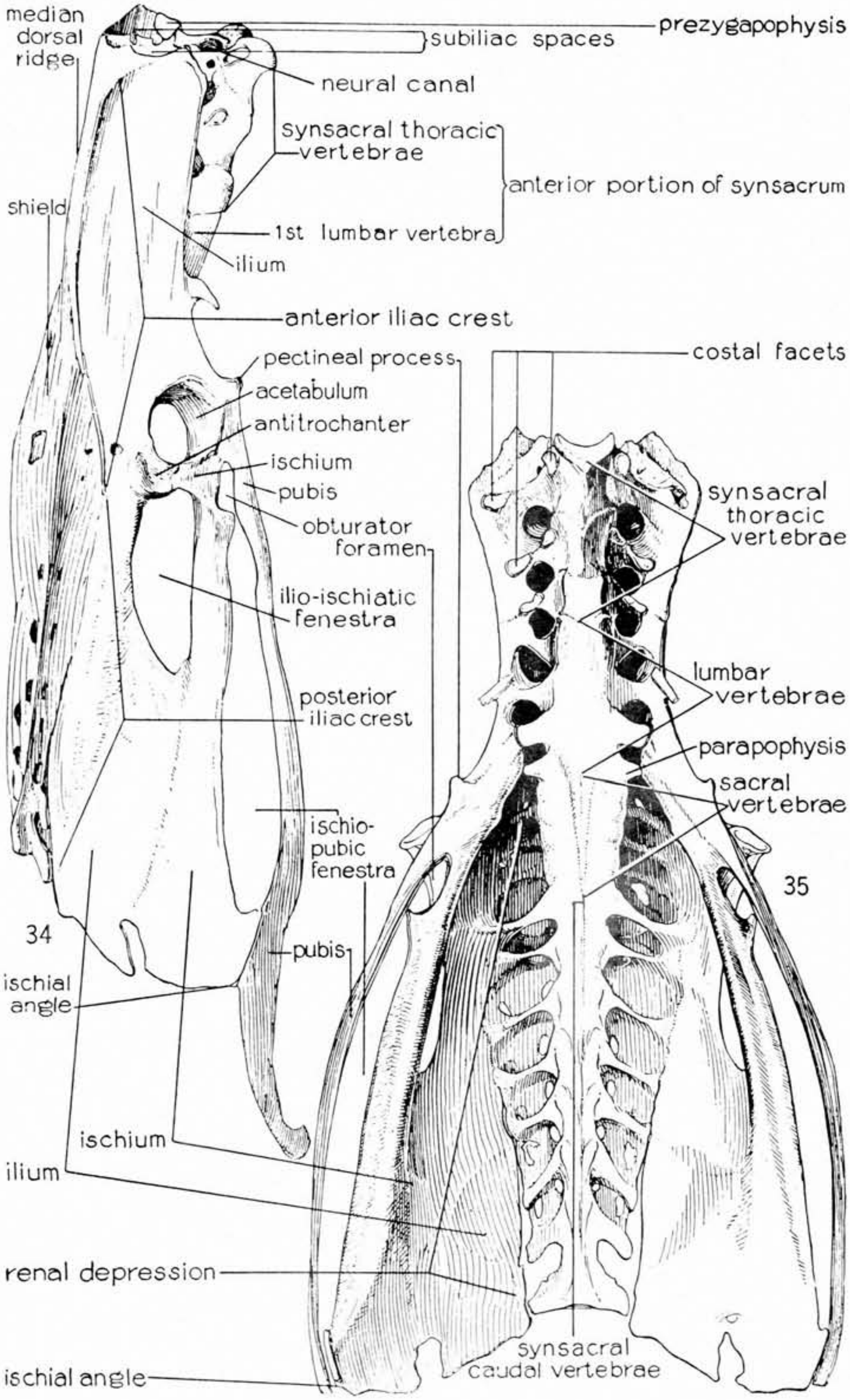
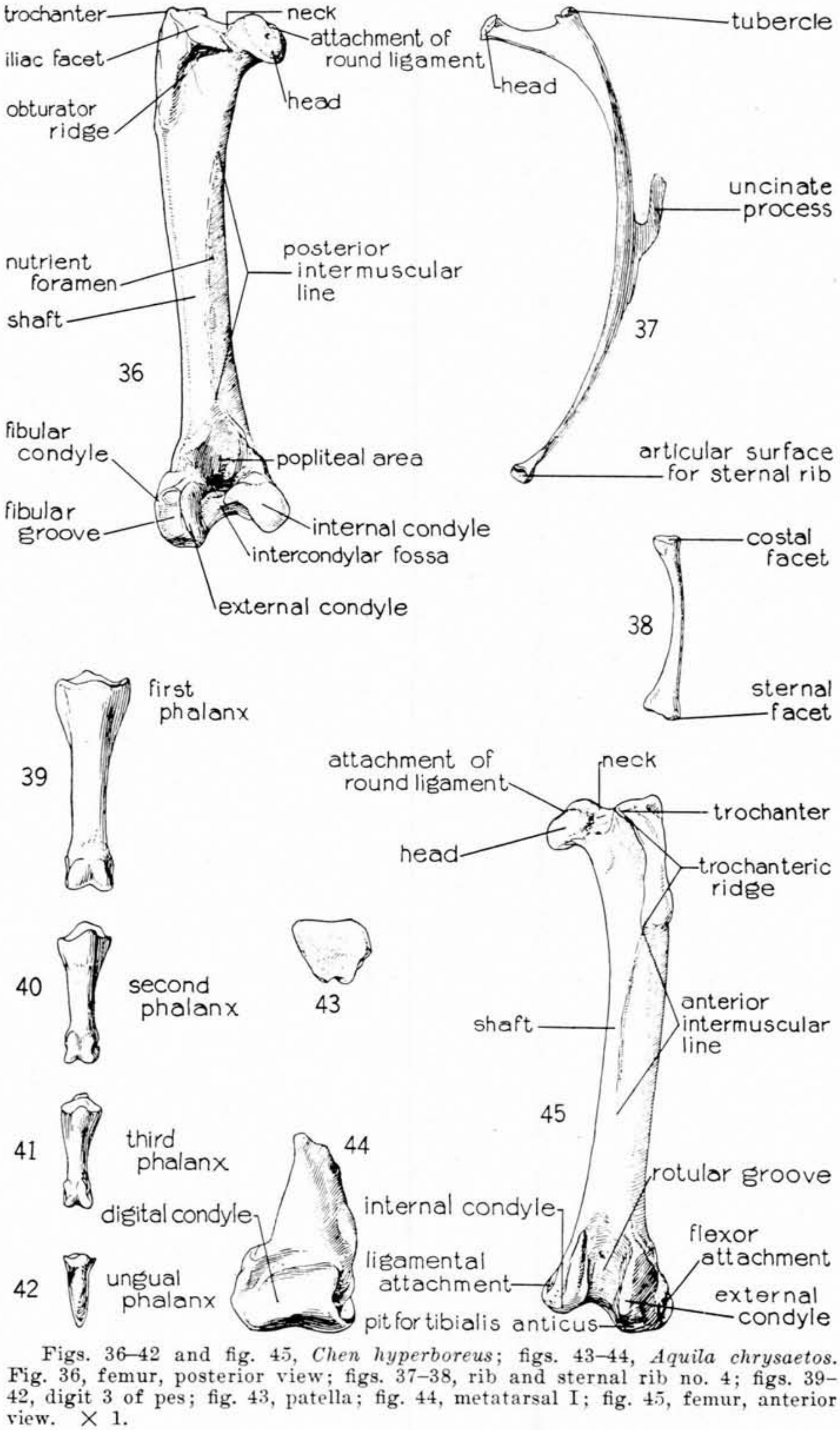
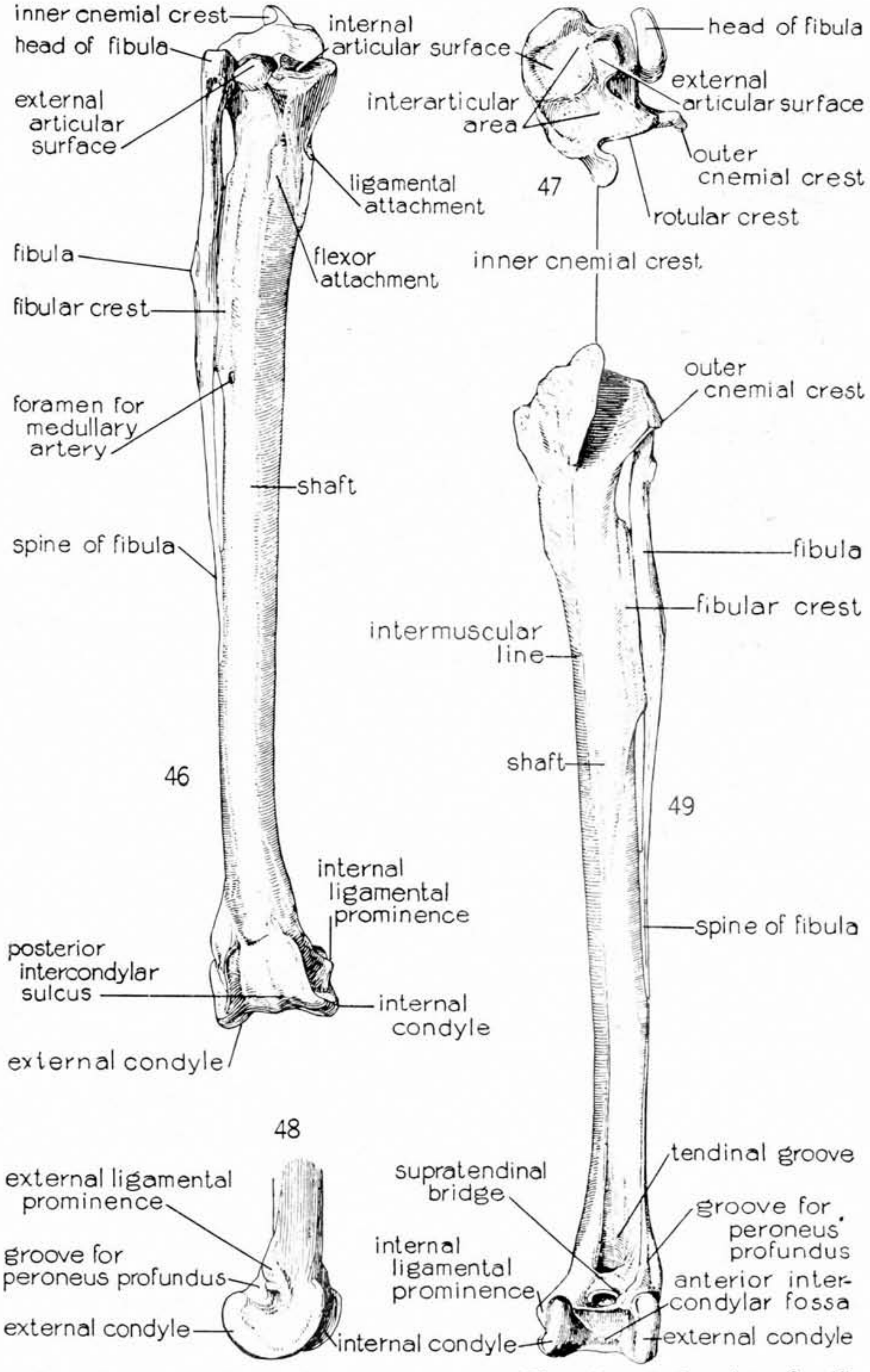
Aquila chrysaetos. Fig. 28, carpometacarpus, internal view. figs. 29–32, phalanges of manus: fig. 29, digit 2, phalanx 1; fig. 30, digit 3; fig. 31, pollex; fig. 32, digit 2, phalanx 2; fig. 33, carpometacarpus, external view. × 1.



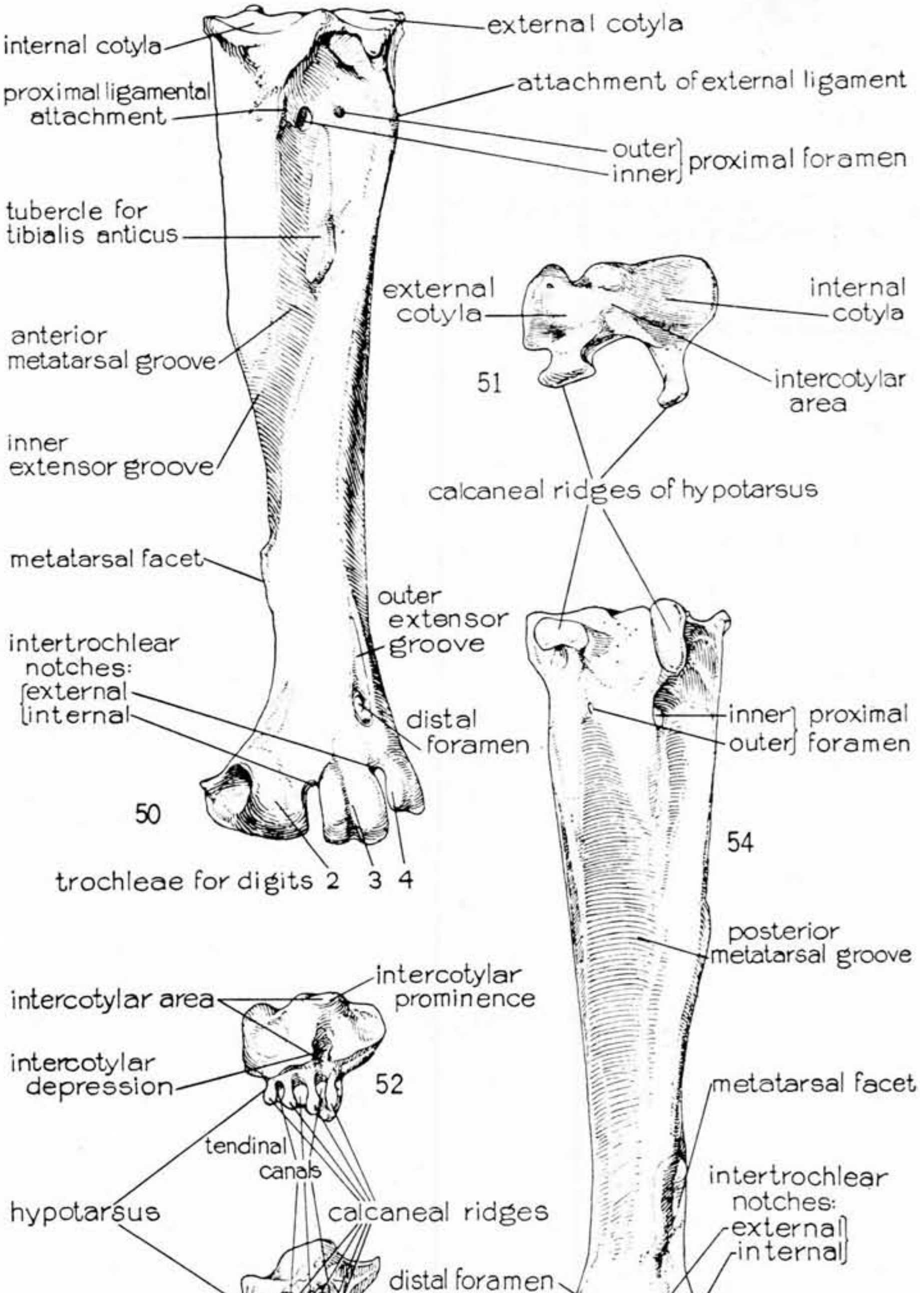
Pelvis of *Chen hyperboreus*. Fig. 34, lateral view; fig. 35, ventral view. × 1.



Figs. 36–42 and fig. 45, *Chen hyperboreus*; figs. 43–44, *Aquila chrysaetos*. Fig. 36, femur, posterior view; figs. 37–38, rib and sternal rib no. 4; figs. 39–42, digit 3 of pes; fig. 43, patella; fig. 44, metatarsal I; fig. 45, femur, anterior view. × 1.



Tibiotarsus and fibula of *Chen hyperboreus*. Fig. 46, posterior view; fig. 47, proximal end, proximal view; fig. 48, distal end, external view; fig. 49, anterior view. × 1.



Tarsometatarsus. Figs. 50, 51 and 54, *Aquila chrysaetos*; figs. 52–53, *Chen hyperboreus*. Fig. 50, anterior view; figs. 51 and 52, proximal end, proximal view; fig. 53, proximal end, posterior view; fig. 54, posterior view. × 1.