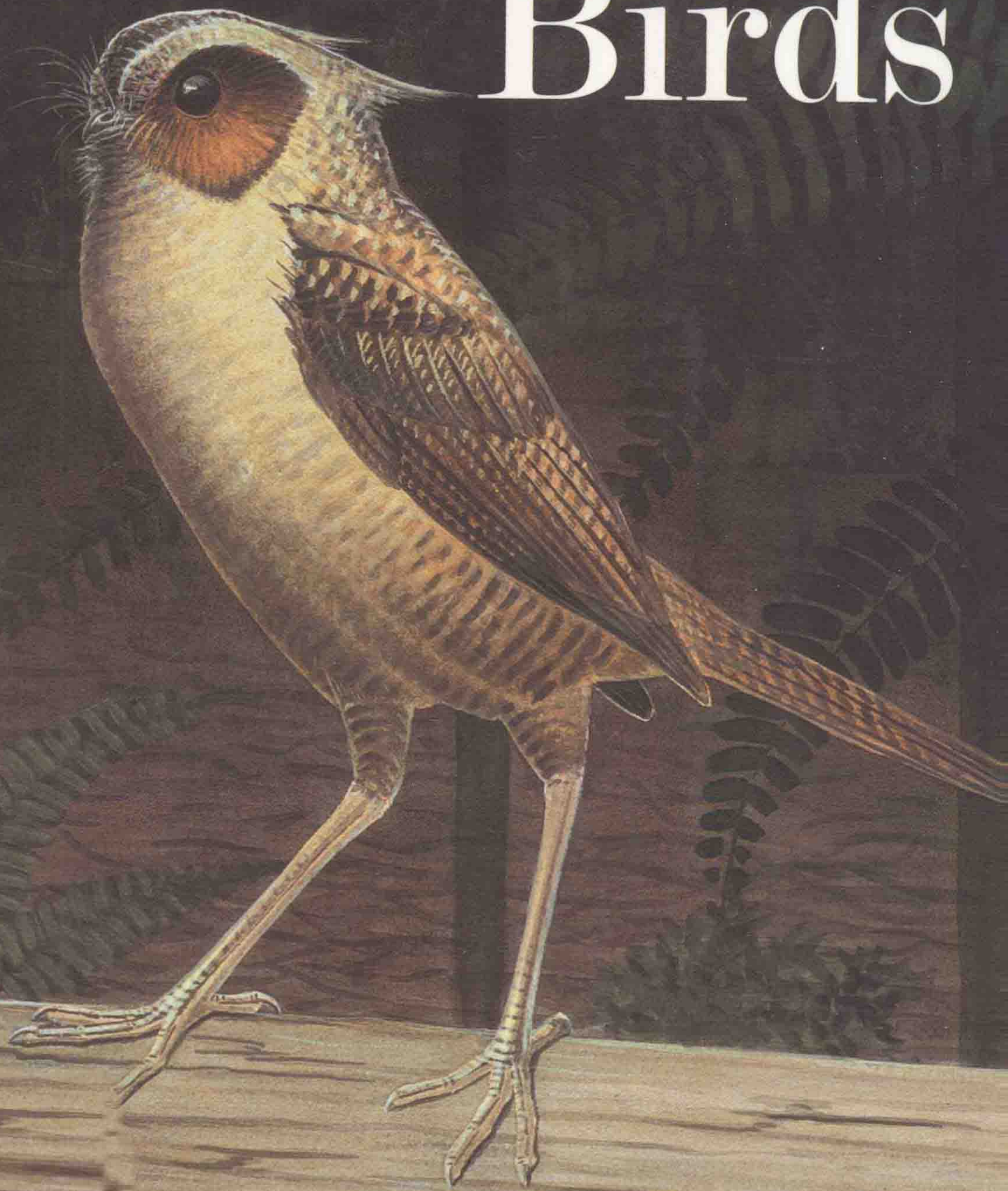


The Origin and Evolution of Birds



ALAN FEDUCCIA

The Origin and Evolution of Birds

Alan Feduccia

Yale University Press

New Haven and London

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Designed by James J. Johnson and set in Aster Roman type by The Marathon Group, Durham, North Carolina. Printed in the United States of America by Vail-Ballou Press, Binghamton, New York.

The paper in this book meets the guidelines for permanence and durability of the Committee on Production Guidelines for Book Longevity of the Council on Library Resources.

Library of Congress Cataloging-in-Publication Data

Feduccia, Alan.

The origin and evolution of birds / Alan Feduccia.

p. cm.

Includes bibliographical references (p.) and index.

ISBN 0-300-06460-8 (hardcover : alk. paper)

1. Birds—Evolution. 2. Birds—Origin. 3. Birds, Fossil.

I. Title.

QL677.3.F43 1996

598.2'38—dc20

95-46758

A catalogue record for this book is available from the British Library.

10 9 8 7 6 5 4 3 2 1

PREFACE

Charles Darwin devoted his life to uncovering the primary mechanism of evolution. In *On the Origin of Species*, published in 1859, he elucidated that mechanism: the principle of natural selection, which provided the motivation that propelled generations of scientists for the quest to uncover evolutionary relations of both plants and animals. Of particular interest here, there began the search for the evolutionary relations of birds, using evidence from paleontology and comparative anatomy. Over the past century evidence from myriad fields—behavior, ecology, physiology, comparative biochemistry, DNA hybridization—have contributed greatly to our understanding of avian relations, but the bedrock of the field has remained paleontology and comparative biology; indeed, paleontology remains the external check for molecular data. This book focuses on the testimony for avian evolution provided from paleontology and comparative biology.

The Origin and Evolution of Birds treats two major themes. The first, presented in chapters 1 through 3, is the discovery of the earliest bird, the *urvogel*, *Archaeopteryx*, and the origin and early evolution of birds and avian flight. The remaining chapters cover the evolution of archaic Mesozoic birds (chapter 4) and modern Tertiary birds (chapters 5 through 8), organized around such themes as the evolution of filter-feeding, flightlessness, raptorial birds, and land birds. The organization is similar to that of my earlier, popular book *The Age of Birds* (Harvard University Press, 1980), and that book served more or less as an outline for this volume.

The field of avian evolution has undergone revolutionary changes in both discovery and theory during the past two decades, often pitting opposing sides in bitter controversy. Nowhere has the vitriole been greater than between those paleontologists who advocate a dinosaurian origin of birds, coupled with the counter-intuitive ground-up, or cursorial, origin of avian flight, and those ornithologists, such as myself, who favor the time-honored and in-

tuitively facile arboreal, or tree-down, theory of the evolution of flight. Many vertebrate paleontologists have accepted a formal, rigid cladistic methodology as the *sine qua non* for reconstructing phylogenies and, using this scheme in an almost religious manner, have discarded geological time as a tool in deciphering evolution, with the result that superficial resemblance often dictates relatedness. To such workers it is inconsequential that birdlike dinosaurs occur some 75 million or more years after the origin of birds. Yet to those more classically trained, like myself, this time gap is a sure sign of convergent evolution, defined simply as the acquisition of similar adaptations in unrelated groups of organisms. Even the names first given to these primarily late Cretaceous birdlike dinosaurs—*Ornithomimus*, the bird-mimic, *Struthiomimus*, the ostrich-mimic, and *Gallimimus*, the fowl-mimic—indicate that their original describers thought that these dinosaurs had independently evolved birdlike features.

Convergent evolution is a central theme of vertebrate history, and it is a predominant thread throughout the avian ranks. Everywhere we look birds from different evolutionary backgrounds have come to look alike: Northern Hemisphere auklets and Southern Hemisphere diving-petrels, great auks and penguins, Old World hornbills and New World toucans, swifts and swallows, Malagasy false sunbirds and true sunbirds, Old World oscine flycatchers and New World suboscine flycatchers—to mention but a few. Although it is relatively easy to uncover superficial, whole-animal resemblance caused by convergence, such as the examples of birds just mentioned, or in vertebrates—fish and dolphins, and bats and pterosaurs—convergence is often so complete, so elusive and subtle, that clues can be difficult to ascertain. One case of massive or whole-animal convergence is that of Mesozoic, toothed divers (*Hesperornis*) and modern loons, and indeed the different development of the proximal end of the tibia was the first clue of nonrelationship, combined with the fact

that the first primitive loon, *Colymboides*, occurs in the Eocene, some 15 or more million years after *Hesperornis*. In early classifications many convergent pairs were placed together, for example, swifts and swallows, and hawks and owls, illustrating that convergence is an insidious and treacherous trap, baited and waiting for the unsuspecting worker.

Nowhere has the trap been more successful than in luring paleontologists to the theropod dinosaurian origin of birds. Theropods, with their bipedal gait and foreshortened arms, superficially resemble flightless birds, especially the ratites, through convergence, and this first led Darwin's champion, Thomas Huxley, to note that "the Dinosaurians are in many important characters intermediate between certain reptiles and certain birds—the birds referred to being the ostrich-tribe" (Darwin 1959). Much more recently, Allison Anders, in an article concerning the convergence between *Tyrannosaurus* and the great flightless bird *Diatryma* (*Natural History*, June 1995), quoted the novelist Flannery O'Connor: "Everything that rises must converge." This is the most important theme of bird evolution.

Just as important, and a discourse of the first part of this book, is that a dinosaurian origin of birds is inextricably linked with the cursorial, or ground-up origin, of avian flight, which is a biophysical impossibility. How could a large, deep-bodied, obligately bipedal reptile, with a long, heavy, balancing tail and greatly foreshortened forelimbs, fighting gravity all the way, give rise to avian flight? The answer, of course, is that it could not. Yet such prestigious institutions as the American Museum of Natural History in New York have recently revised their entire dinosaur hall to conform to this theory, and their accompanying book *Discovering Dinosaurs* (Norell, Dingus, and Gaffney, 1995), proclaimed that "the smallest dinosaur is the bee hummingbird . . . found only on Cuba" (25). They, like many others who adhere to a rigid cladistic methodology, have been led into that perfidious trap of convergence that lies camouflaged and waiting for the unsuspecting victim. I join many others in generally accepting the tenets of cladistic theory, that only shared, derived features can indicate relatedness, but the implementation of cladistic methodology is where the intractable problems are encountered. Often the procedure is more like a board game than a careful scientific examination of anatomy, and simple tallies of characters by computer are used to determine who is related to whom. As a consequence, convergence is almost impossible to weed out. Within birds, cladistic methods have grouped such unrelated and disparate forms as the ancient, toothed hesperornithiform divers and loons, and even hawks and owls. It is not enough to state simply that the closest relatives of hawks remain un-

known, there must be a hypothesis of relationship, and until another better scheme is published, then it remains as the supposed best genealogy. But does science really work that way? Often there is simply insufficient evidence to offer such bold hypotheses, and cladograms confer an aura of truth to what is in reality speculation. For example, we do not know the closest relatives of hawks; but does this mean that they are related to owls by default? Such is the case for the origin of birds. Paleontological cladists claim that opponents of the theropod origin must produce a more suitable ancestor, but alas, we simply don't have sufficient evidence. We can only say, as dictated by science and logic, that the ancestor was surely a small, quadrupedal, arboreal archosaur, a pre-dinosaur in the overall scheme of the genealogy.

The idea of a theropod origin of birds originally became coupled with the idea, now largely disproven, of hot-bloodedness or endothermy, in dinosaurs, the idea being that hot-blooded dinosaurs became coated with feathers for insulation, sprouted wing feathers on the arms, and flew off into the sunset. Proclaimed one author of the first known bird, "*Archaeopteryx* supports two theories: warm-blooded dinosaurs and the dinosaurian ancestry of birds"! However, although the theory of hot-bloodedness has fallen from favor, the advocates of a theropod origin of birds still reconstruct earthbound dinosaurs with a feathered coat, defying logic, as the feathers of birds that have lost the ability to fly invariably degenerate and become hairlike in appearance.

The Mesozoic era, we have just begun to understand and as I discuss in chapter 4, was a period of adaptive radiation of many archaic groups of birds that became extinct at the end of the Cretaceous. Predominant in this radiation were the recently discovered "opposite," or enantiornithine, birds, so named because the three metatarsal bones fused from proximal to distal, the opposite direction of that of modern, ornithurine birds. The enantiornithines were quite diverse, but were all characterized by a well-developed, precocious flight apparatus but a primitive, urvogel-style pelvic region and hindlimbs. These opposite birds are included in the same subclass, the Sauriurae, with the urvogel, *Archaeopteryx*, but the lineage of modern-type birds, the Ornithurae, as current evidence tells us, evolved at about the same time as the Sauriurae, the early Cretaceous, and is represented by such early forms as the Mongolian *Ambiortus* and the Chinese wader *Gansus*. Other Mesozoic ornithurines included the toothed divers, the hesperornithiforms, and the ichthyornithiforms, but all of these groups became extinct at the close of the Cretaceous, along with the myriad groups of reptiles and other organisms.

The fossil record of birds now tells us clearly that:

(1) the Cretaceous-Tertiary boundary event was very significant for birds; this is a recent discovery, but surely, with all the life-forms that became extinct, the analogy of the miner's canary should tell us that birds would be the first to be affected; (2) the diversification of modern orders was post-Mesozoic; almost all modern orders thought to be present in the Cretaceous have now been shown to be enantiornithines, yet all modern orders are known from Eocene deposits; (3) the early Tertiary diversification was explosive: no modern orders are present at the close of the Cretaceous, but all are present by the Eocene; if this evidence is valid, then all modern orders may have arisen explosively during a period of some 5 to 10 million years, and with this many-stranded genealogy, relationships of modern orders may well be lost to the past; and (4) the mammalian fossil record provides a good model for avian diversification; that the mammalian radiation should serve as a model for bird evolution is eminently logical.

As I mentioned above, I treat the Tertiary radiation of birds in an unconventional manner, by exploring such themes as filter-feeding and wading birds, the evolution of flightlessness, the evolution of birds of prey, and the rise of land birds. In each chapter specific topics illustrate themes of evolution—for example, flightless birds illustrate such concepts as the mode and tempo of evolution, as well as many features of flight, which can be studied by examining what happens in the flightless state.

One outcome of the revelation that the modern avian orders are post-Cretaceous is the recognition that there exist numerous living fossils within the modern avifauna ranging across the spectrum of the class Aves. To mention a few, tinamou-like birds are an offshoot of the lineage that led to the ratites, tropicbirds are primitive, basal pelecaniforms, the Australian freckled duck, *Stictonetta*, is primitive, as is the Australian magpie-goose, *Anseranas*, and the South American screamers are an early offshoot of the anseriform birds. Continuing, the South American seriarnas are primitive gruiforms and were no doubt basal to the carnivorous phorusrhacids, and many of the monotypic genera within the Gruiformes, such as the finfoots and sunbitterns, are surely ancient relicts. Rollers and Malagasy ground-rollers (Coraciidae and Brachypteraciidae) were common birds of the Eocene, as were primitive piciform relatives of the puffbirds, mousebird-like birds, and varied caprimulgiforms. Indeed, the island of Madagascar may well be an avian refugium of the early Tertiary, with its ground-rollers, cuckoo-roller, and mesites, just as it is for such mammalian relicts as the lemurs, and its preservation, seriously threatened today, is absolutely essential. The conservation of many of these avian relicts all over the world should indeed be of great concern, as the

modern avifauna provides us with a living laboratory of the early Tertiary avian radiation.

This book owes a large debt to a large number of individuals, all of whom cannot be mentioned here. However, I would like to acknowledge the following for their invaluable help: Herculano Alvarenga, Allison Andors, Philip Ashmole, Ian Atkinson, Herman Berkhoudt, Walter Bock, Walter Boles, José Bonaparte, Michael Brett-Surman, Alan Brush, Eric Buffetaut, Paul Bühler, Kenneth Campbell, Robert Carroll, Robert Chandler, Sankar Chatterjee, Jacques Cheneval, Luis Chiappe, Anusuya Chinsamy, Leslie Christidis, Richard Cifelli, Nicholas and Elsie Collias, Charles Collins, A. H. Cramer, Arthur Cruickshank, Nina Cummings, Michael Daniels, Ron Dorfman, Carla Dove, Steve Edinger, Andrzej Elzanowski, Robert Farrar, C. Hilary Fry, Stephen Gatesy, Ed Gerken, Paul Germain, Frank Gill, John Goss-Custard, Lance Grande, Mark Hallett, Alan Harris, Dave Harris, Bernd Haubitz, Hartmut Haubold, Max Hecht, W.-D. Heinrich, Angelika Hesse, Richard Hink, Lian-hai Hou, Peter Houde, Helen James, Robert Johnson, Philip Kahl, Bill Kelley, Lloyd Kiff, Evgeny Kurochkin, Roxie Laybourne, Karel Liem, David Ligon, Larry Marshall, Beverly McCulloch, Gordon Maclean, Don Merton, David Meyer, Carlo Morandini, Cécile Mourer-Chauviré, Martin Moynihan, Giuseppe Muscio, Åke Norberg, Ulla Norberg, Rory O'Brien, John Ostrom, Kenneth Parkes, Raymond Paynter, Jr., Colin Pennycuik, Stefan Peters, François Poplin, Robert Raikow, Pat Rich, Siegfried Rietschel, John Ruben, Dale Russell, Peter Ryan, José Sanz, Gary Schnell, Paul Sereno, Christopher Shaw, Bernard Sigé, Robin Simpson, David Steadman, Burkhard Stephan, Peter Stettenheim, Robert Storer, Stuart Strahl, Clark Sumida, Sam Tarsitano, Tim Tokaryk, Michael Tove, James Vanden Berge, Günter Viohl, Alick Walker, Glenn Walsberg, Doug Wechsler, Peter Wellnhofer, Rupert Wild, Wolfgang Wiltschko, Lawrence Witmer, Derek Yalden, Zhonghe Zhou, and Gert Zweers. I thank the many museums and institutions that contributed illustrations, including the American Museum of Natural History, Bavarian State Collection of Paleontology and Historical Geology, Bishop Museum (Honolulu), Black Hills Institute of Geological Research, Bürgermeister Müller Museum (Solnhofen), Canterbury Museum (Christchurch), Carnegie Museum of Natural History, Field Museum of Natural History, George C. Page Museum (Los Angeles), Humboldt University Museum für Naturkunde (Berlin), Jura-Museum (Eichstätt), Museum of Comparative Zoology (Harvard), Museum of New Zealand (Wellington), National Geographic Society, Natural History Museum of Los Angeles County, New York Zoological Society,

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Senckenberg Museum (Frankfurt), National Museum of Natural History (Smithsonian), and Peabody Museum of Natural History (Yale).

I especially acknowledge my highly esteemed colleagues Larry Martin of the University of Kansas and Storrs Olson of the Smithsonian Institution, who over the years have stoked the fires of enthusiasm and helped clarify many important issues. I also wish to thank Dr. Dorothy S. Fuller, sister of George Miksch Sutton, who kindly arranged for her late brother's pen-and-ink bird drawings to be used in this book. Much credit is also due

Susan Whitfield, artist-illustrator in the Department of Biology at the University of North Carolina, Chapel Hill, who rendered many of the illustrations, particularly line drawings and cladograms. My friend and colleague John P. O'Neill of Louisiana State University skillfully rendered the frontispieces for the eight chapters, as well as other pen-and-inks. Yale University Press also deserves credit for putting together a difficult project, in particular Science Editor Jean Thomson Black, who enthusiastically sought the manuscript, and Laura Jones Dooley, whose skilled editing led this book to completion.

The Origin and Evolution of Birds



Archaeopteryx displaying in a late Jurassic ginkgo. Although *Archaeopteryx* has been envisioned as a cursorial predator, most evidence indicates that it was primarily a primitive arboreal bird and a trunk climber and that it does not represent a terrestrial stage in the evolution of avian flight and feathers. (Drawing by John P. O'Neill)

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FEATHERED REPTILES

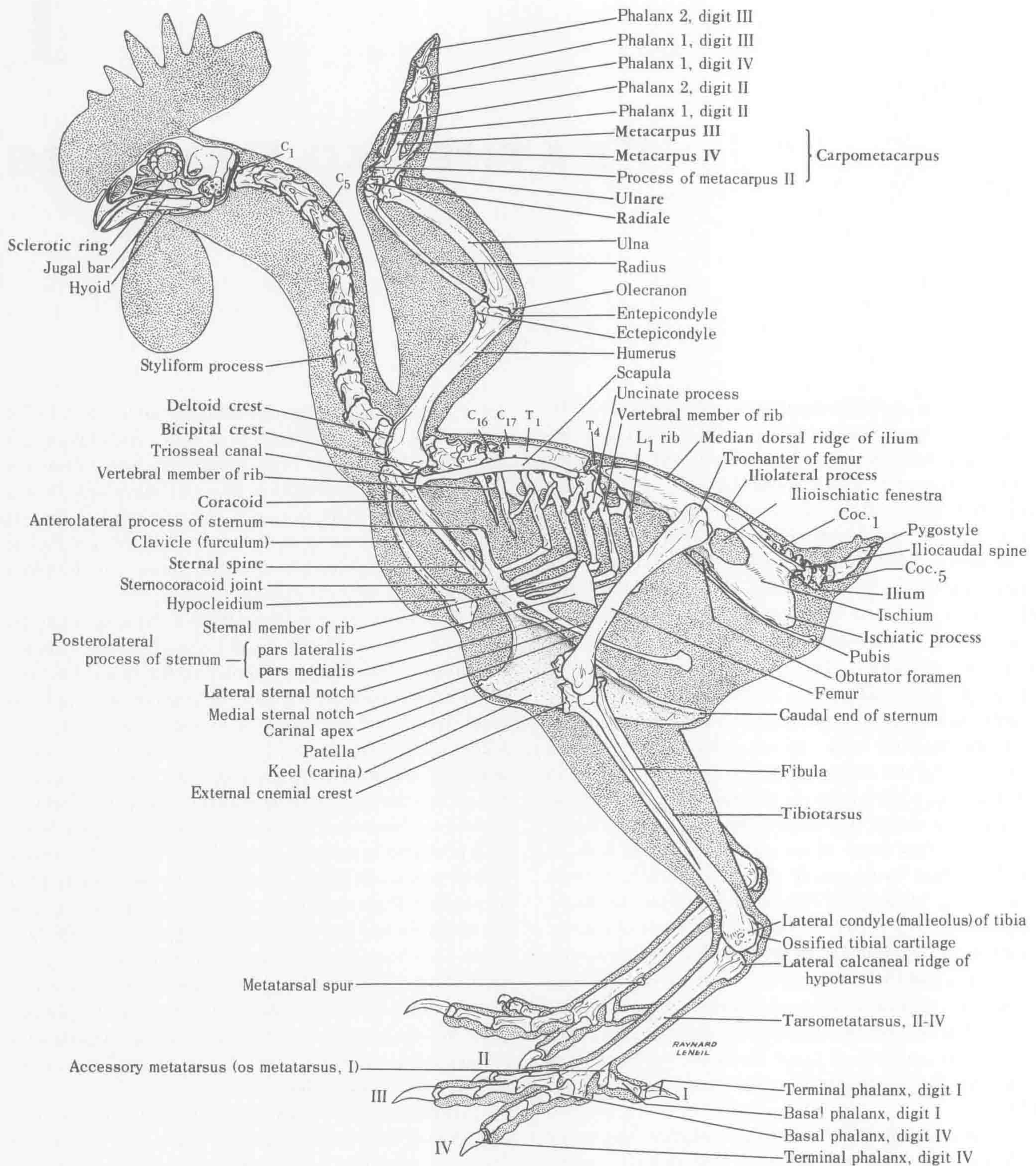
At a time when tropical temperatures warmed much of the Northern Hemisphere and low, palmlike vegetation covered what is now central Europe, a feathered creature the size of a crow met its death in a shallow lagoon. Of the event itself this is all we can know, separated from us as it is by approximately 150 million years. But the death is recorded nonetheless, chronicled by sediments that, throughout the millennia, settled and consolidated into lithographic limestone, a fine-grained limestone that preserved not only the shape of the bones but the delicate impression of feathers. The creature thus memorialized was *Archaeopteryx lithographica*, and, though indisputably birdlike, it could with equal truth be called reptilian. The forearms that once held feathers ended in three fingers with sharp, recurved claws. The *Archaeopteryx* fossil is, in fact, the most superb example of a specimen perfectly intermediate between two higher groups of living organisms—what has come to be called a “missing link,” a Rosetta stone of evolution. Its discovery in 1861, just two years after publication of Charles Darwin’s *On the Origin of Species* (1859), seemed an unparalleled act of cosmic good will toward science, for by fulfilling the Darwinian expectation that such intermediate forms existed, this one fossil had a profound influence on the ultimate acceptance of the concept of evolution through natural selection. And for students of avian evolution, *Archaeopteryx* became the focal point of efforts to determine the descent of birds.

In attempting to construct a genealogical history, or phylogeny, for birds, we must look both to living forms and to the fossil record of ancient birds. *Archaeopteryx*, the oldest avian form yet discovered, is represented by a feather and seven skeletal specimens, several of which, notably the famous Berlin specimen, are almost perfectly preserved. But the fossil record is rarely so cooperative. Most bird bones are hollow and thin walled—adaptations that lighten the skeleton for flight—and are therefore not

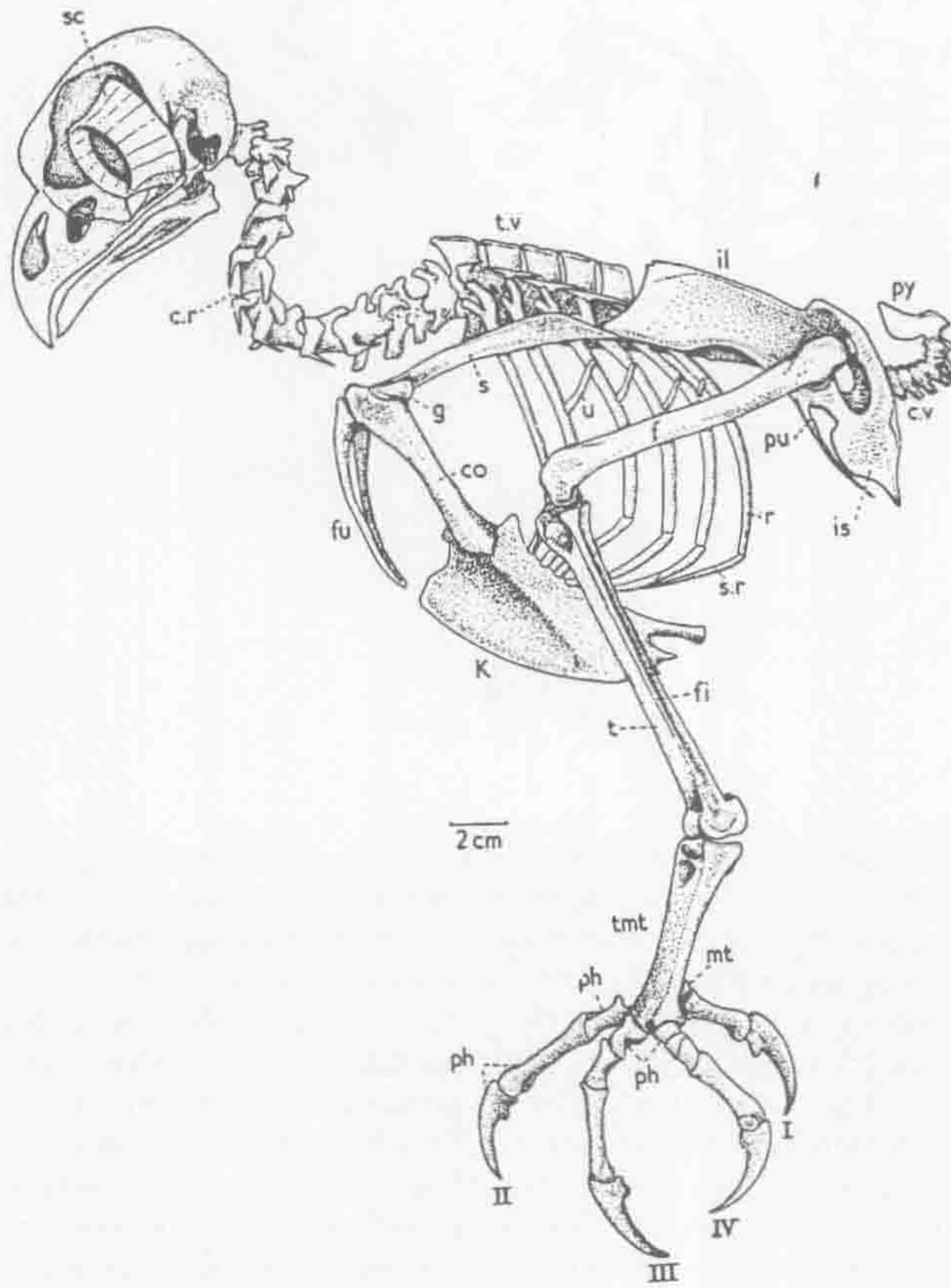
easily preserved. An extreme example of this is seen in the frigatebird, whose feathers, it is said, probably weigh more than the dried skeleton. True or not, it does illustrate the point that bird fossils are formed from fragile bones, are often fragmentary, or consist of single bones. Although bird fossils are sometimes abundant, only the rare find of an associated skeleton allows major advances in the effort to establish evolutionary relationships.

One could, technically, establish a phylogeny of birds, or any other group, exclusive of the fossil record, and perhaps have a reasonably good idea of the major lineages using evidence from such diverse areas as anatomy and biochemical and genetic (DNA) comparisons. Yet, even then, problems are legion. Not only is there considerable argument about the methodology that should be employed, but the search for meaningful anatomical features (known as characters) that elucidate relationships is laden with problems because, beneath their feathers, birds tend to look very much alike anatomically. In order for flight to be possible, flight architecture was invented early on and the forelimbs had to assume an elongated form in the first birds. That basic form has been retained with very little modification in all modern birds. Mammals, by contrast, possess many features, such as teeth, that differ substantially among the various groups and indicate evolutionary relationships. Traits of the major avian groups, as we shall see, present few such clues.

Because of the extremely restrictive physiological and anatomical demands of flight, birds are finely tuned metabolic machines, with very high metabolic rates and constrained aerodynamic morphologies. This restrictive aerodynamic design means that birds are the most structurally uniform of all vertebrate orders. Evolutionary biologist Walter Bock (1963a) has argued convincingly that if birds are to fly, they must conform to a narrow set of structural and physiological requirements, and so slight morphological divergence has been the characteristic feature



The skeleton of the male domestic chicken (*Gallus*), showing the major features of the avian skeleton. (Adapted from Lucas and Stettenheim 1972; courtesy Peter Stettenheim)



Skeleton of the eagle owl (*Bubo bubo*) with the wings removed. Note that the fibula extends the entire length of the tibia. Structures on the left side only are shown except for the right clavicle. Abbreviations: *co*, coracoid; *c.r.*, cervical rib; *c.v.*, caudal vertebrae; *f*, femur; *fi*, fibula; *fu*, furcula (fused clavicles); *g*, glenoid; *il*, ilium; *is*, ischium; *k*, sternal keel; *mt*, first metatarsal; *ph*, phalanx; *pu*, pubis; *py*, pygostyle; *r*, vertebral rib; *s*, scapula; *sc*, sclerotic rings (scleral ossicles); *s.r.*, sternal rib; *t*, tibiotarsus; *tmt*, tarsometatarsus; *t.v.*, thoracic vertebrae; *u*, uncinate process; *I-IV*, digits. (From Bellairs and Jenkin 1960; courtesy Academic Press)

of their primary and secondary adaptive radiations. Flight is, in a morphological sense, the biomechanically and physiologically most restrictive vertebrate locomotor adaptation, permitting little latitude for new designs. Ground-dwelling tetrapods, such as terrestrial mammals, and swimming forms, such as fishes, have not been so constrained in their structure by extreme physiological demands or aerodynamic constraints, and as a consequence more morphological divergence has characterized their adaptive radiations. As an analogy, an engineer can construct a terrestrial vehicle in diverse configurations, but there is really only one basic design for fixed-wing aircraft. Unlike mammals, which possess ample features such as teeth that vary considerably between the various groups, the higher categories of birds present few such clues to their interrelations. As a result, many of the major lineages

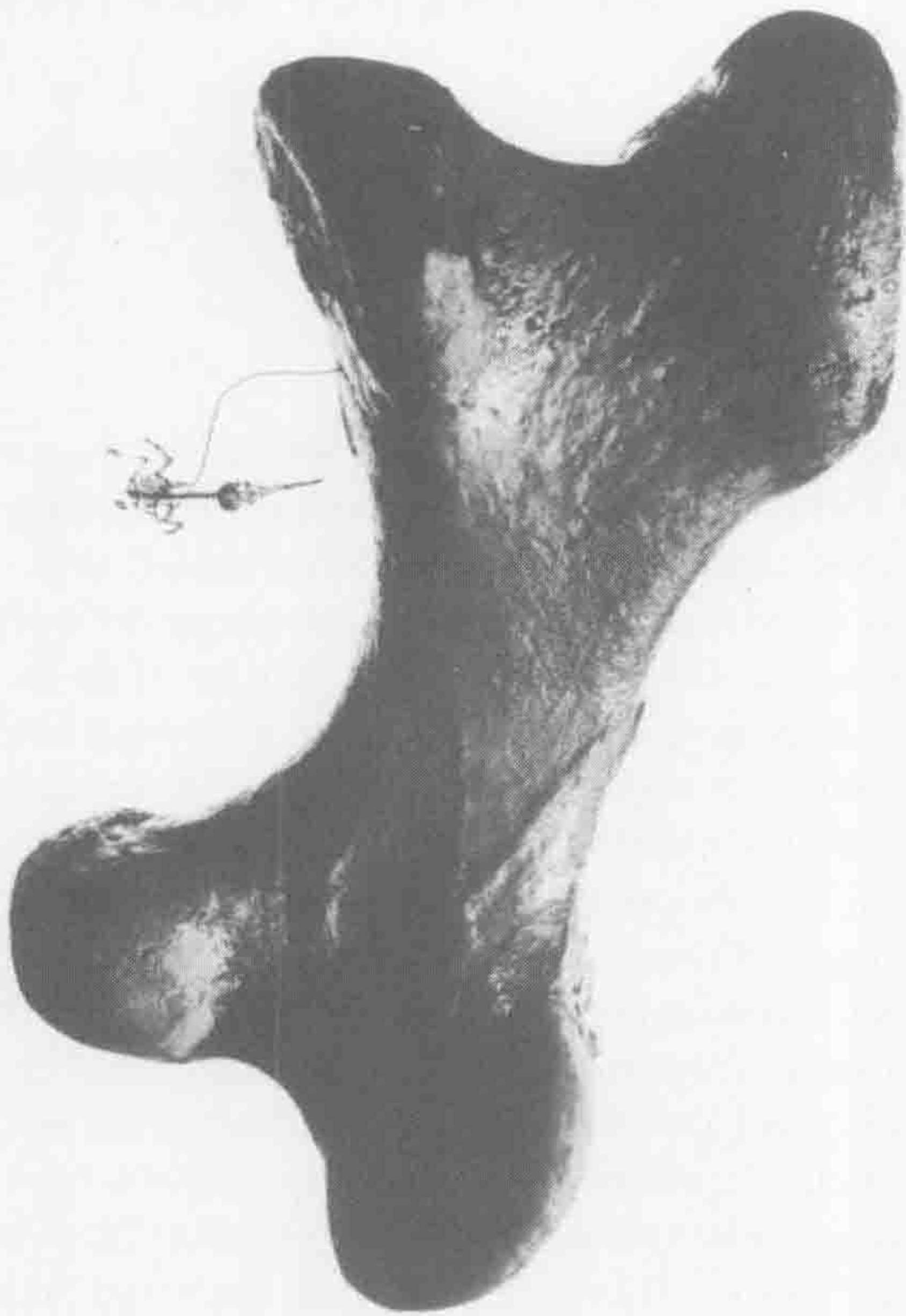
of birds are defined on one or a handful of diagnostic anatomical features.

Small Size and Light Weight

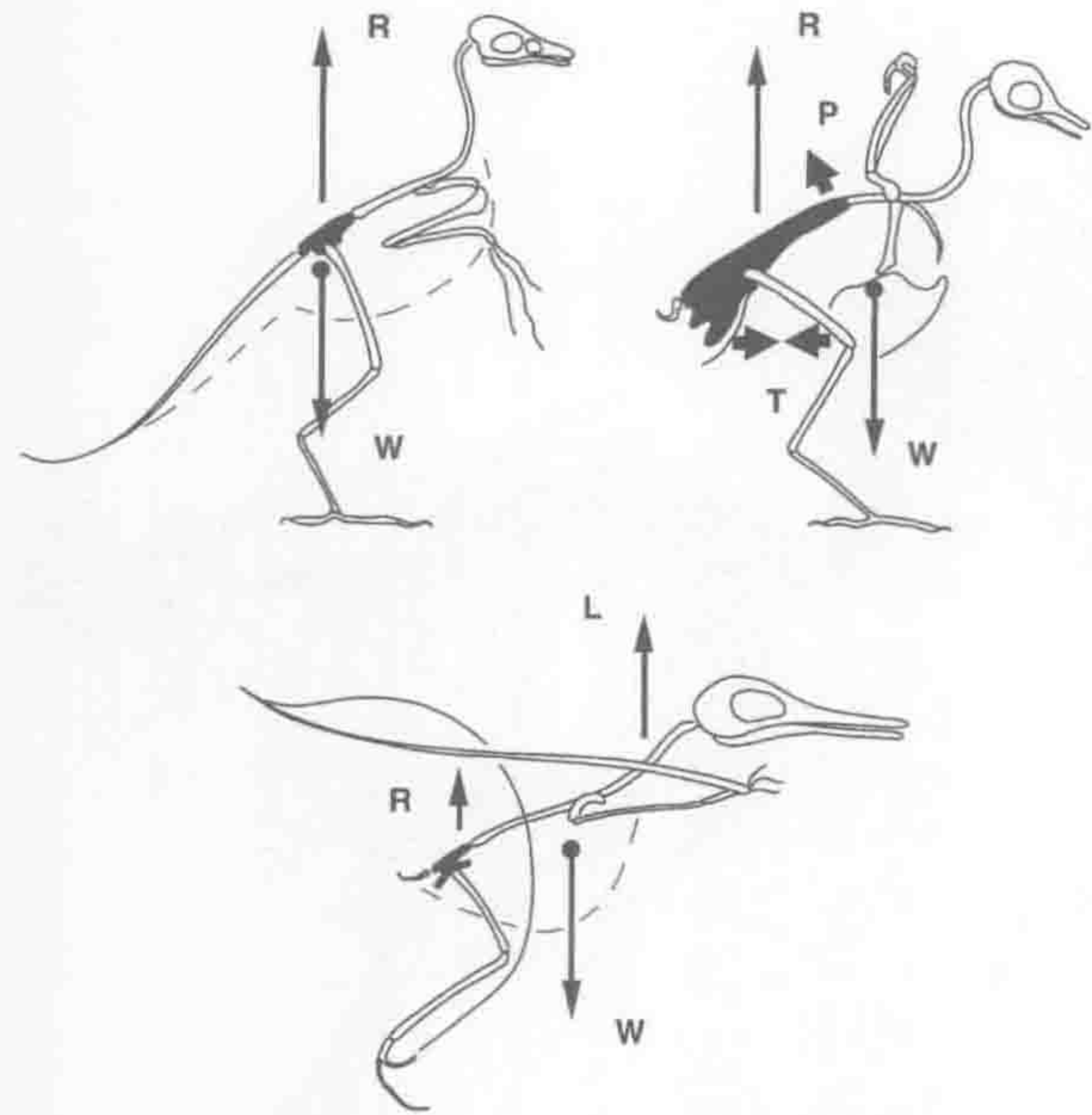
As we shall see, small size is essential for the evolution of flight, for only in small animals could the original, rudimentary protofeathers have had an aerodynamic effect, and small size can be viewed as a general characteristic of birds. Although such conspicuous birds as ostriches and penguins capture the attention of the public, in reality, the vast majority of the some 9,700 living bird species (Sibley and Monroe 1990) weigh much less than a kilogram (2.2 lbs.) and are fewer than 50 centimeters (20 in.) in length (Proctor and Lynch 1993). In fact, although there were some exceptionally large flying birds, such as the extinct New World teratorns, which probably depended on winds to get aloft, the upper limit of mass in normal flying birds is represented by such types as the large bustards, storks, and swans, approaching some 16 or so kilos (35 lbs.). As well as being lightweight, the avian body is compact. Body mass is concentrated between the wings and the center of gravity, which hangs below the wings to convey aerodynamic stability. This is accomplished by lodging the major flight muscle mass—comprising up to 40 percent of body weight—on the sternum.

Because it is dogma that the avian body is characterized by light weight, Prange, Anderson, and Rahn surprised the ornithological world when they presented data to support a conclusion that, “contrary to common expectations, the skeletons of birds are not lighter than those of mammals” (1979, 105). But they merely showed that the allometry of skeletal mass to body mass in birds is very similar to that in mammals. Allometry refers to relative growth in which the proportions of a particular structure change as overall size changes. The more interesting question revolves around the relation of weight to volume. As Paul Bühler has noted, “At the same time that selection pressure diminishes the weight of a skeleton, it probably also diminishes, to a certain degree, the weight of the soft parts of the body. So, the constant skeleton mass to body mass relation does not indicate that the avian skeleton in general is as heavy as the mammalian skeleton” (1992, 391–392). Indeed, one need only pick up the skull of a nightjar in one hand and the skull of a mammal of similar body size in the other to confirm this expectation. As we shall see, in addition to overall lightening, weight has been redistributed in the avian body: with birds’ loss of teeth, the gizzard gained importance as the masticatory organ, and as flight was perfected, the major flight muscles comprised a disproportionate amount of the body’s weight.

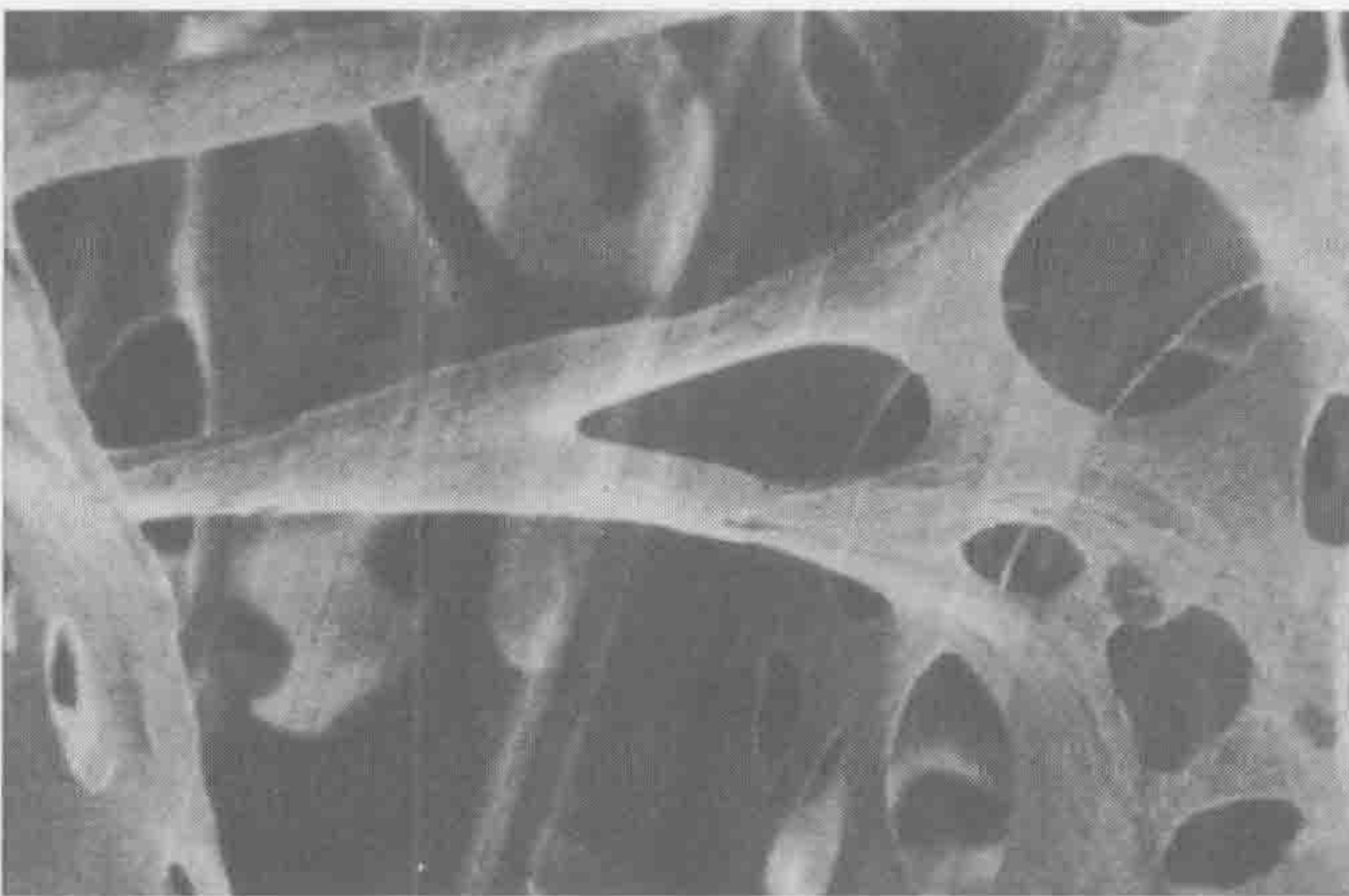
Many anatomical traits are unique to modern birds



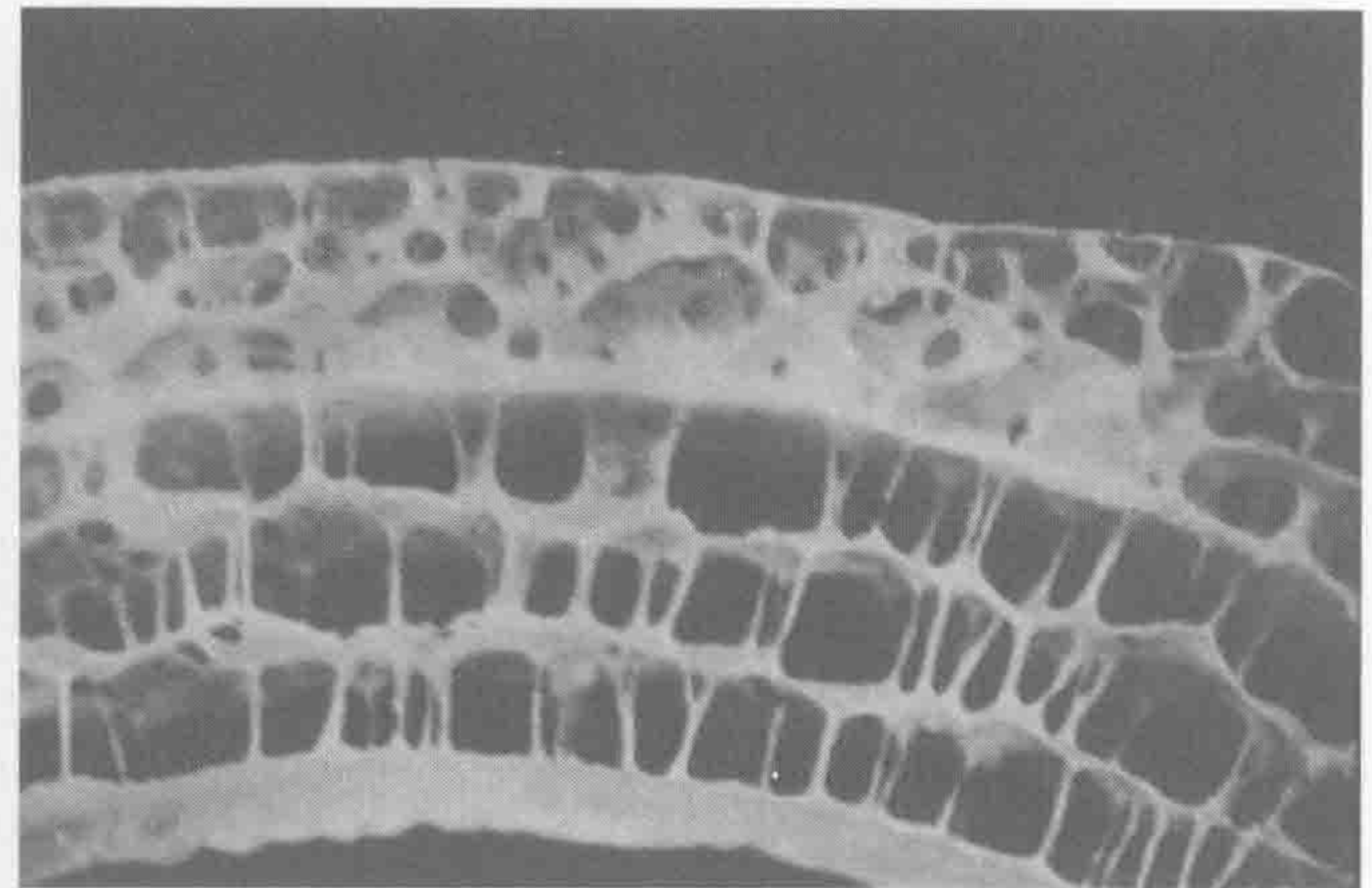
Hummingbird skeleton and the hollow femur (thigh bone) of an extinct Malagasy elephantbird (*Aepyornis*), illustrating each end of the avian size spectrum. The bee hummingbird (*Mellisuga helenae*), at 6.4 cm (2.5 in.) and 2.5 gm (1/10 oz.), is the smallest extant bird, whereas elephantbirds are estimated to have been up to 3 m (9.8 ft.) tall and to weigh up to 450 kg (1,000 lbs.). (Courtesy Department of Library Services, American Museum of Natural History)



In *Archaeopteryx* (top left), the long tail allowed the body weight (W) to act along approximately the same line as the upward reaction from the hip joint (R). Modern birds (top right) have lost the tail, and the body weight therefore acts ahead of the hip joint, tending to topple the body forward. This is resisted by the enormously expanded, shoehorn-shaped synsacrum, which works as a lever. Tonic muscles (T) pull the posterior end of the synsacrum toward the femur, and this in turn holds the anterior end of the body up (P). The later pterosaurs (bottom) also lost the tail but did not develop a similarly expanded synsacrum. They had no adaptation to permit movements to be balanced about the hip joint in bipedal standing. A running take-off might have been possible, as shown, with part of the weight supported aerodynamically (L) by the wings. (Modified from Pennycuik 1986)



Scanning electron micrograph of a forked bony beam from the interior of the braincase wall of the tawny owl (*Strix aluco*), illustrating the best-known weight-reducing strategy in birds: the substitution of air for marrow or marrowlike tissue in the cavities of bones as well as in the skull. Section in image 1 mm wide. (From Bühler 1992; courtesy Los Angeles County Museum of Natural History, Science Series 36)



Four-story construction of the braincase of a long-eared owl (*Asio otus*), illustrating the "sandwich" construction in the walls of the avian braincase. This is one of the most visually impressive weight-reducing strategies in birds. (From Bühler 1992; courtesy Los Angeles County Museum of Natural History, Science Series 36)

and have evolved as adaptations for flight. The major bones are hollow and pneumatized, with direct connections to an extensive air-sac and respiratory system; such bones as the lightweight, hollow humerus are exemplary of this structural complexity. In addition, such bones as the vertebrae, skull, and jaws have undergone pneumatization. Lightweight, pneumatized skull bones are perhaps best exemplified in owls and nightjars, where broadening of the braincase is accomplished by air-filled "sandwich" bone (Bühler 1992). Many bones of modern birds have also been fused or deleted, more than in any other group of living vertebrates (but closely paralleling the extinct pterosaurs); these adaptations are also associated with lightening of the skeleton to permit flight. In most birds, the fibula, too, is reduced to a splint along the outer tibiotarsus. Bird embryos have a full-length fibula, but it is generally reduced through ontogeny, or embryological development (owls are an exception); birds also parallel pterosaurs in this feature. As one might expect, the first known bird, *Archaeopteryx*, had a fibula that ran the full length of the tibia. However, like modern birds, *Archaeopteryx* had thin-walled hollow bones with a thickness within the range of variation of modern birds, and it exhibited pneumatization in the braincase (Bühler 1992).

Distinctive Attributes of Birds

Small size and light weight are general features of birds, but their salient features include feathers, the avian-type furcula (the wishbone, or fused clavicles), and a reversed first toe known as the hallux. Other diagnostic features are anatomical traits involved in feeding and locomotion—the skull, the beak, and skeletal structures involved in flight, perching, and running, including the feet, the wings, and a miscellany of odds and ends.

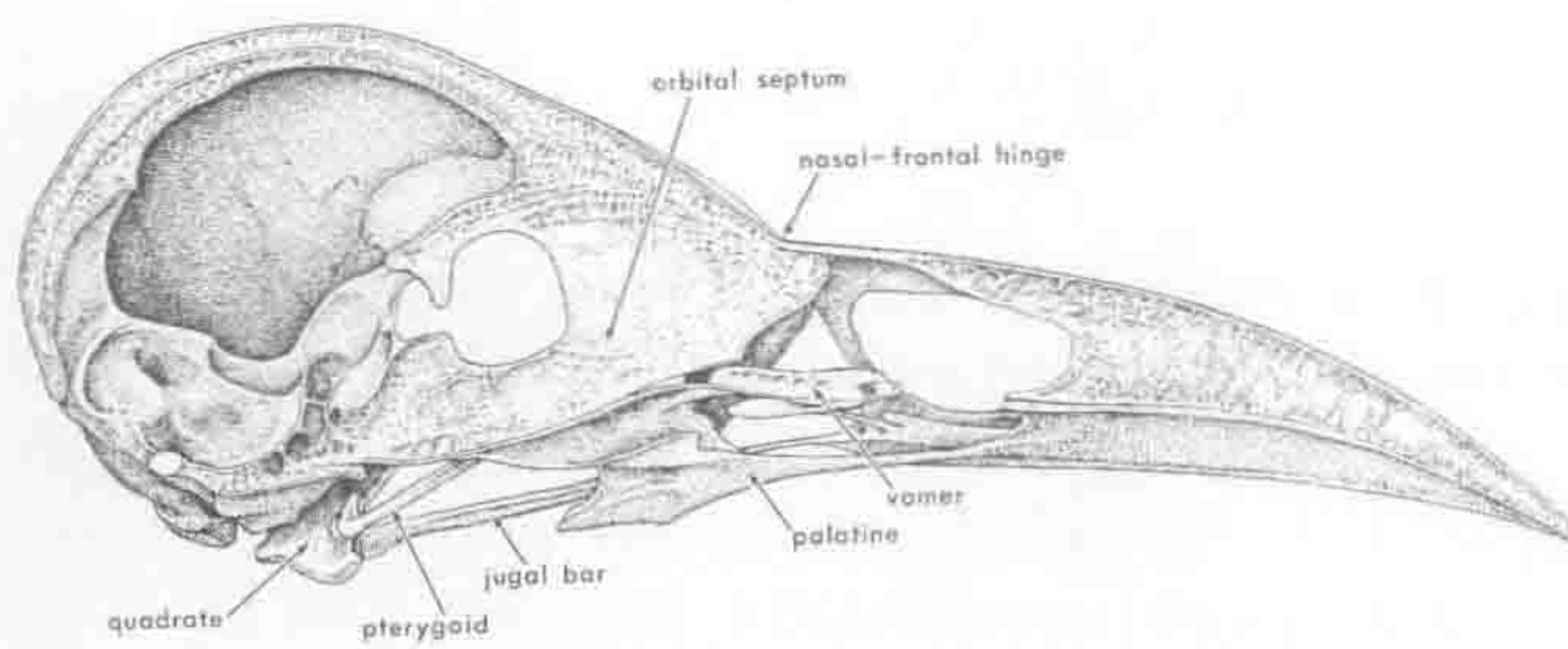
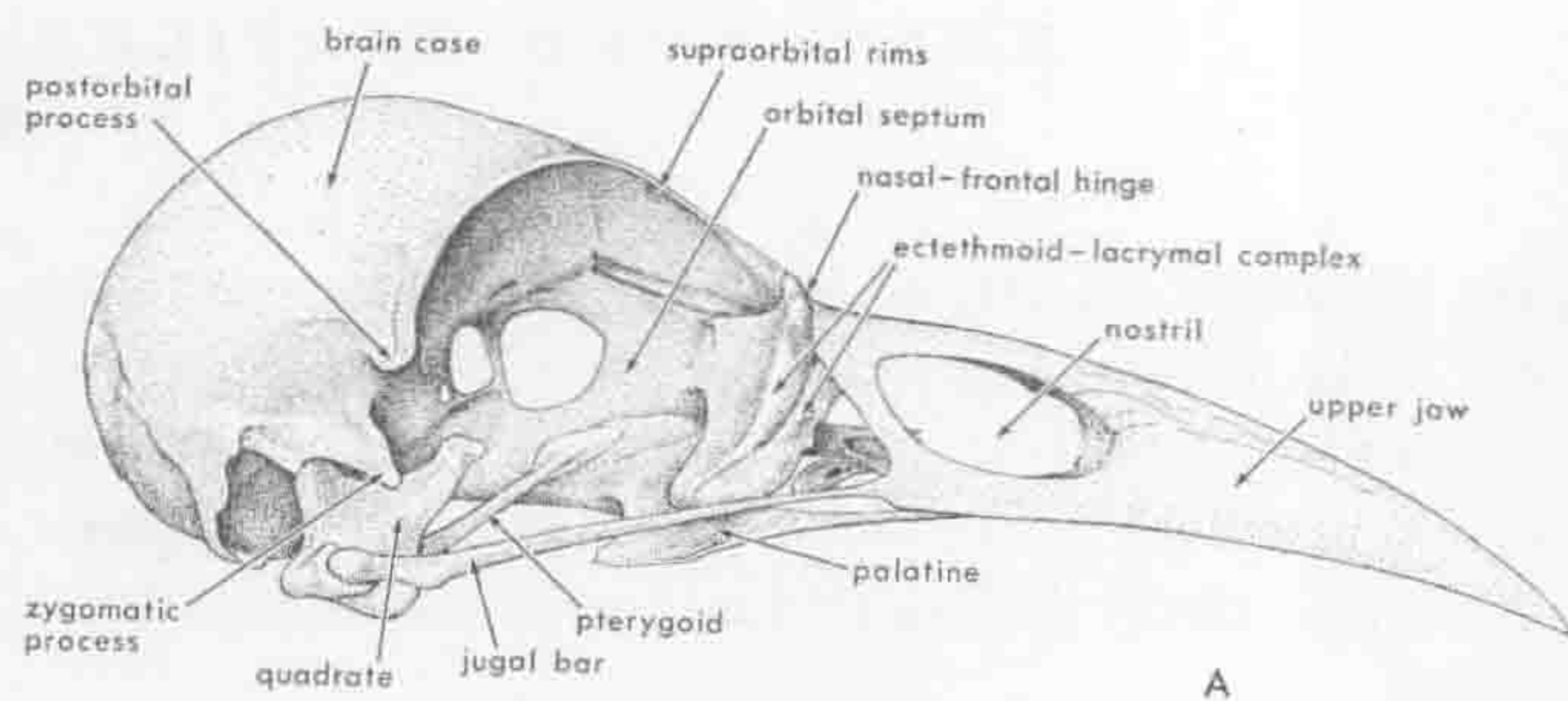
The Avian Skull. The first birds had a full complement of uniform reptilian teeth in upper and lower jaws, but over time these were reduced and eventually lost. Cretaceous toothed divers, the hesperornithiform birds (see chapter 4), illustrate an intermediate stage of avian reduction of teeth in which the premaxilla lacked teeth and the teeth of the upper jaw were restricted to the maxilla; ultimately, the entire tooth row and maxilla were lost. The toothed jaws were transformed into the lighter bill or beak. The modern beak is covered with a horny sheath, a keratinized thickening of epidermal corneum called the rhamphotheca, a usually hard and rigid, highly adaptable, often plastic structure transformed into everything from a nutcracker in finches and grosbeaks to an instrument for tearing flesh in hawks and owls. Much of the work accomplished in mammals by the mammalian jaw, with its com-

plex heterodont dentition and grinding molars, is taken over in birds by the muscular gizzard, often augmented by grinding, with the ingestion of grit and gizzard stones. As much as 2.3 kilos (5 lbs.) of grit and stones have been recovered from the individual gizzards of fossilized moas.

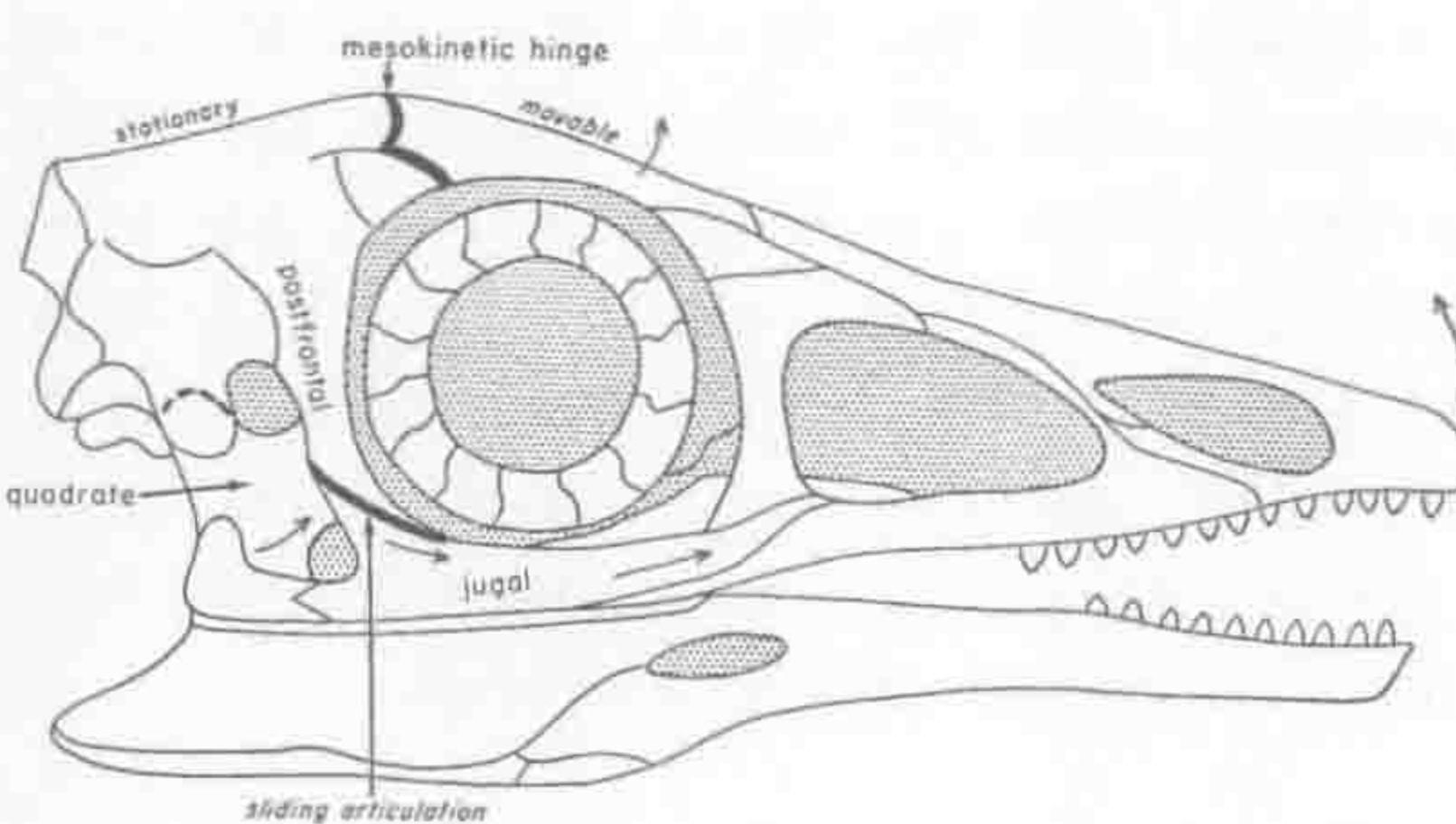
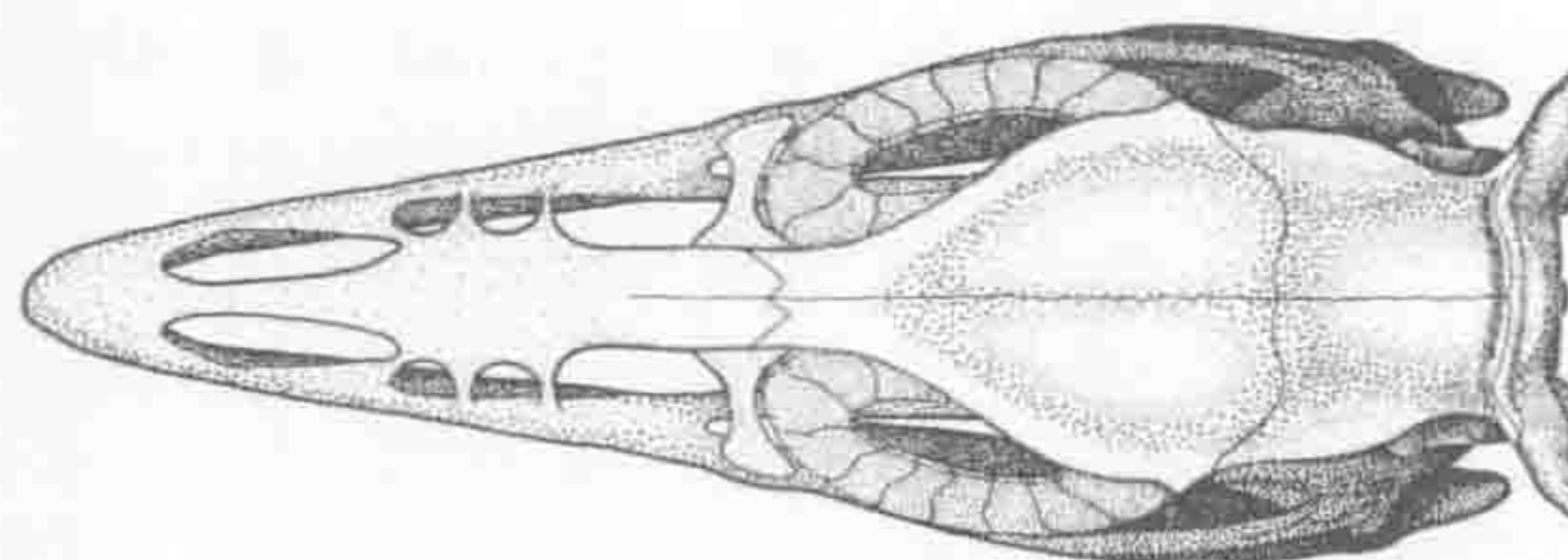
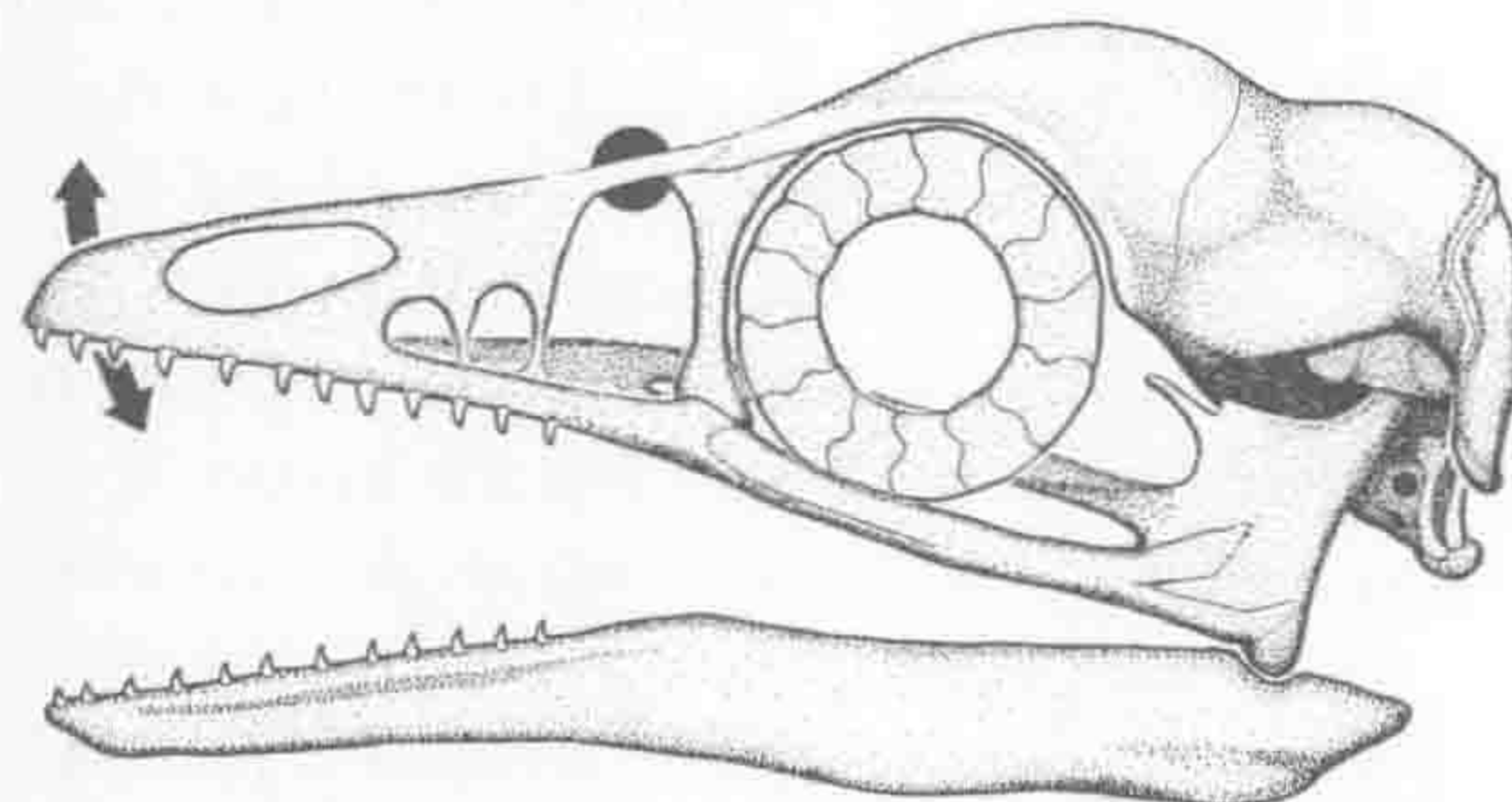
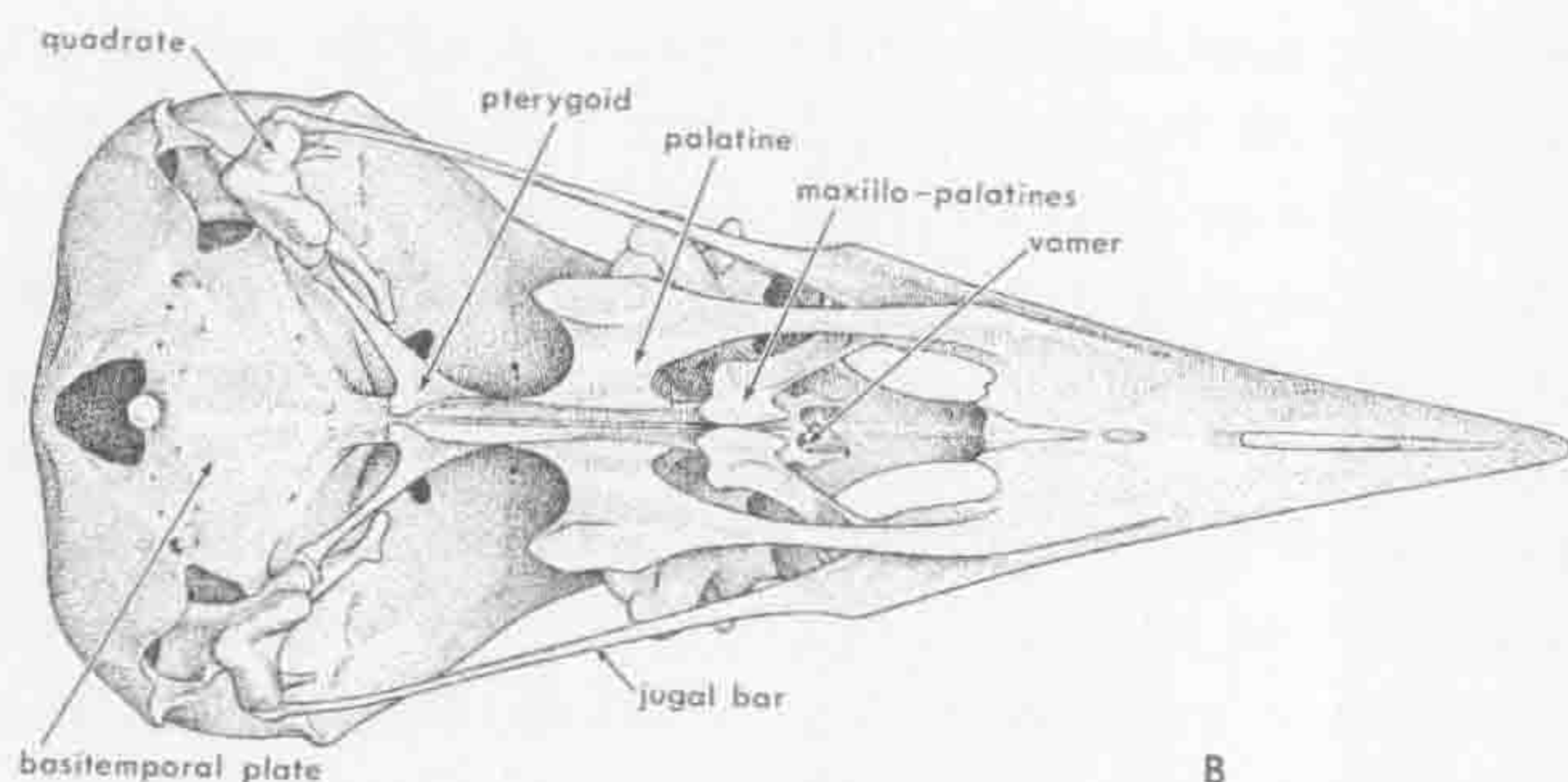
The bird skull is reptilian in many respects, with its single occipital condyle and movable quadrate, which articulates with the lower jaw. However, the general proportions of the avian skull are governed by the much larger relative size of the brain and eyes, and the avian brain fills the cavity of the braincase quite tightly, rather than being separated from it by loose tissue, as in reptiles. Also, the avian skull has a unique form of cranial kinesis—the movement of all or part of the upper jaw relative to the braincase, a universal feature in birds (Bock 1964). The dorsoventral swing of the upper jaw relative to the braincase results in, among other things, a larger gape and a faster closing, more efficient jaw mechanism and permits the bill to maintain a more or less stationary axis as the jaws open and close, thus enhancing birds' ability to capture prey. Cranial kinesis as such is not unique to birds and is also found among fishes, fossil amphibians, and reptiles.

Genital Organs. Aside from skeletal modification, myriad adaptations of the bird's anatomy reduce overall weight, including the sex organs: most females have but one ovary, and many males lack a penis, although a penis-like intromittent organ has been reacquired by some large flightless birds, such as the ostrich, as well as by tinamous, most waterfowl, storks, and curassows, and a smaller organ is found in chickens and turkeys. Because most birds lack external genitalia, copulation normally involves only a brief cloacal contact in which sperm is transferred. All birds lay eggs—that is, they are oviparous—and, in fact, birds are the only vertebrate class to have no members that are viviparous, giving birth to live young (Blackburn and Evans 1986).

Fusion, Deletion, and Skeletal Rigidity. The avian body is extremely compact. Almost all the major skull bones are fused into a single rigid structure, the wing and leg bones are reduced in number, and many elements are fused. The wing, for example, has three instead of the normal five fingers of the vertebrate hand. From this three-fingered hand emerge the primary flight feathers, numbering from nine to twelve in flying birds; from the ulnar region come the secondary flight feathers, sometimes, but by no means always, attached to the ulna by individual bony knobs known as ulnar quill knobs (Edington and Miller 1941; Yalden 1985). Collectively, the flight feathers are called remiges (singular, remex).

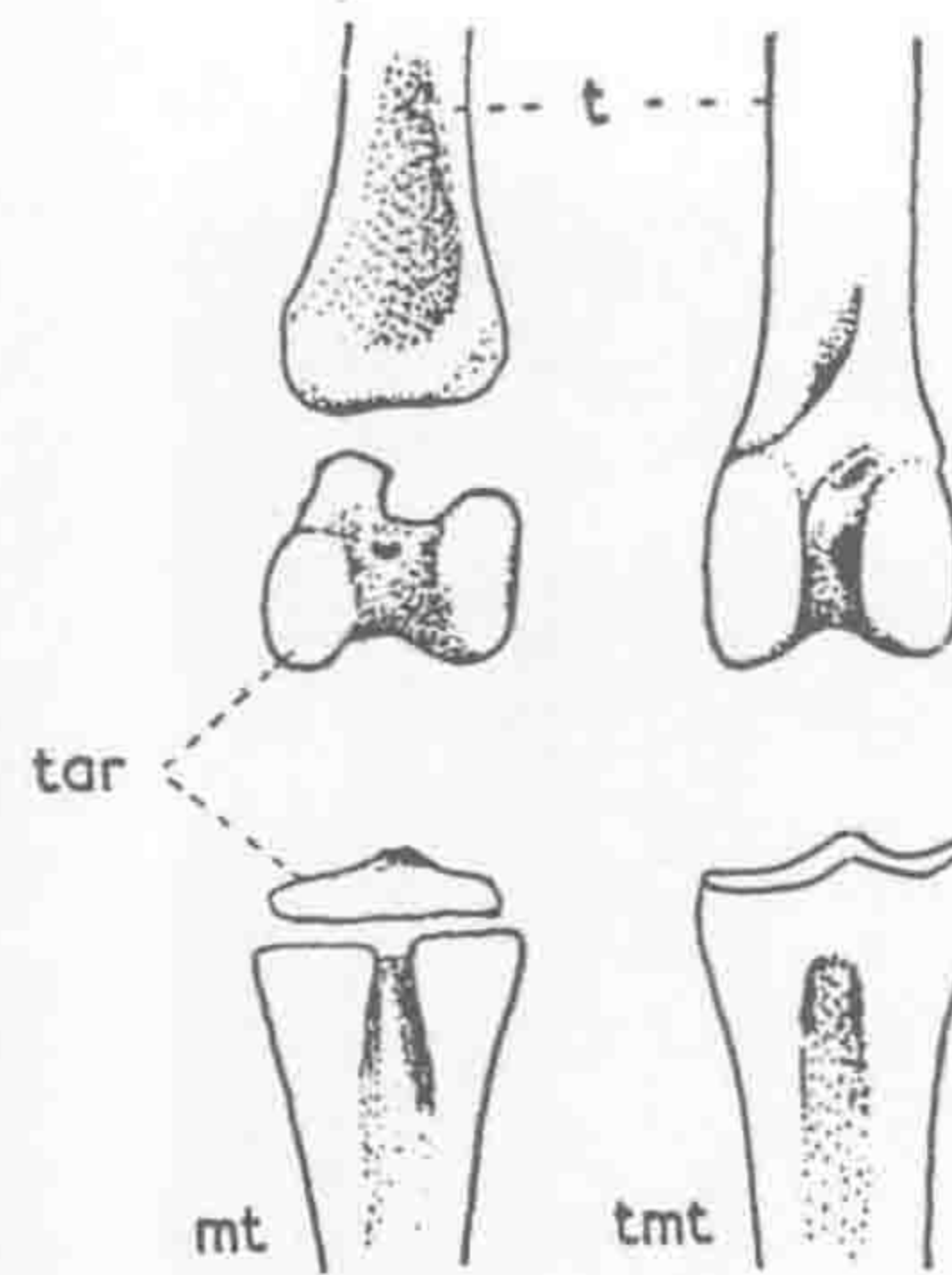
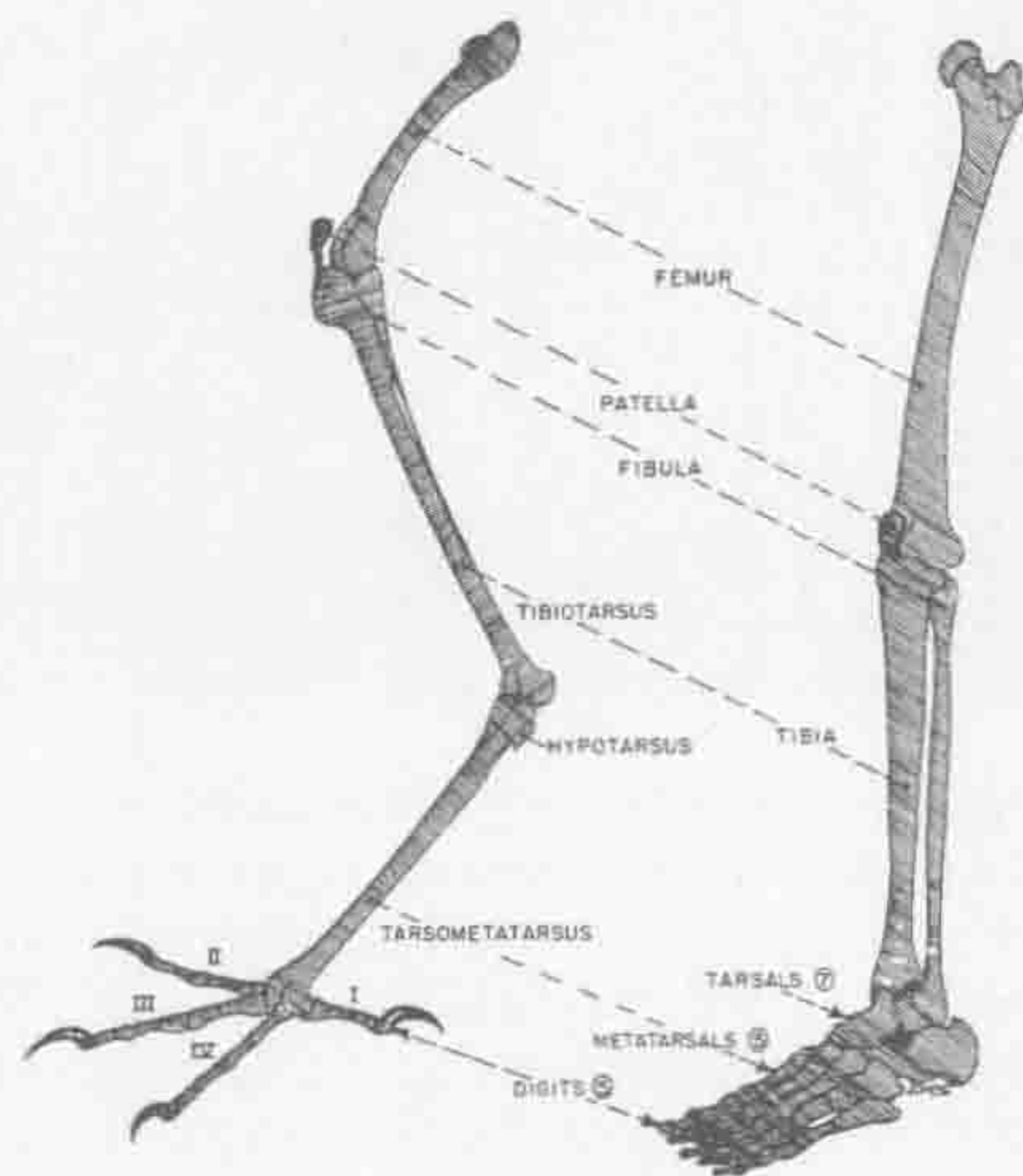
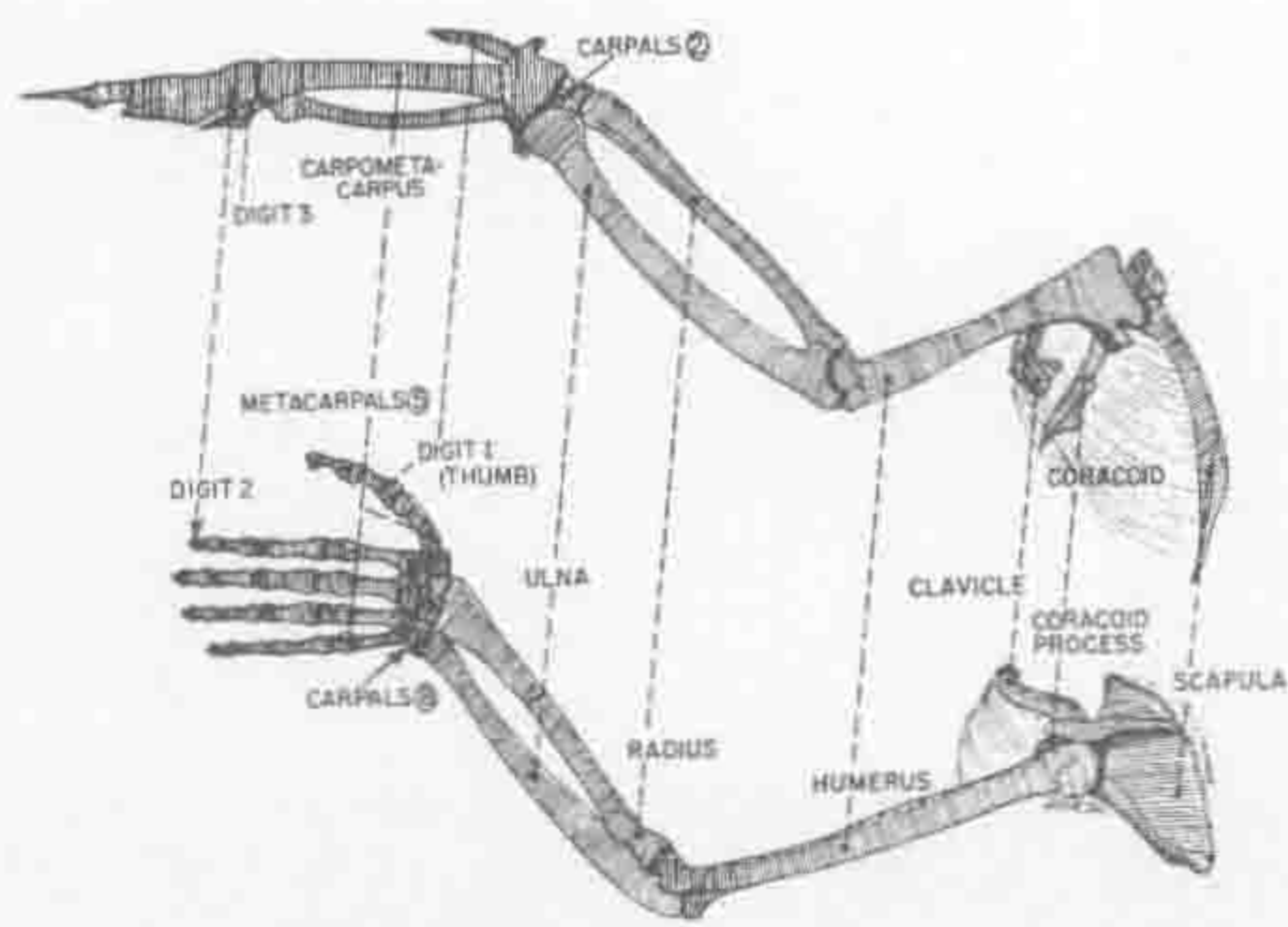


Left, Skull of a crow (*Corvus*) seen from the side (A) and from beneath (B). Above, skull of a crow cut along the midsagittal plane. (From Bock, *Journal of Morphology*, copyright © 1964; reprinted by permission of John Wiley and Sons)



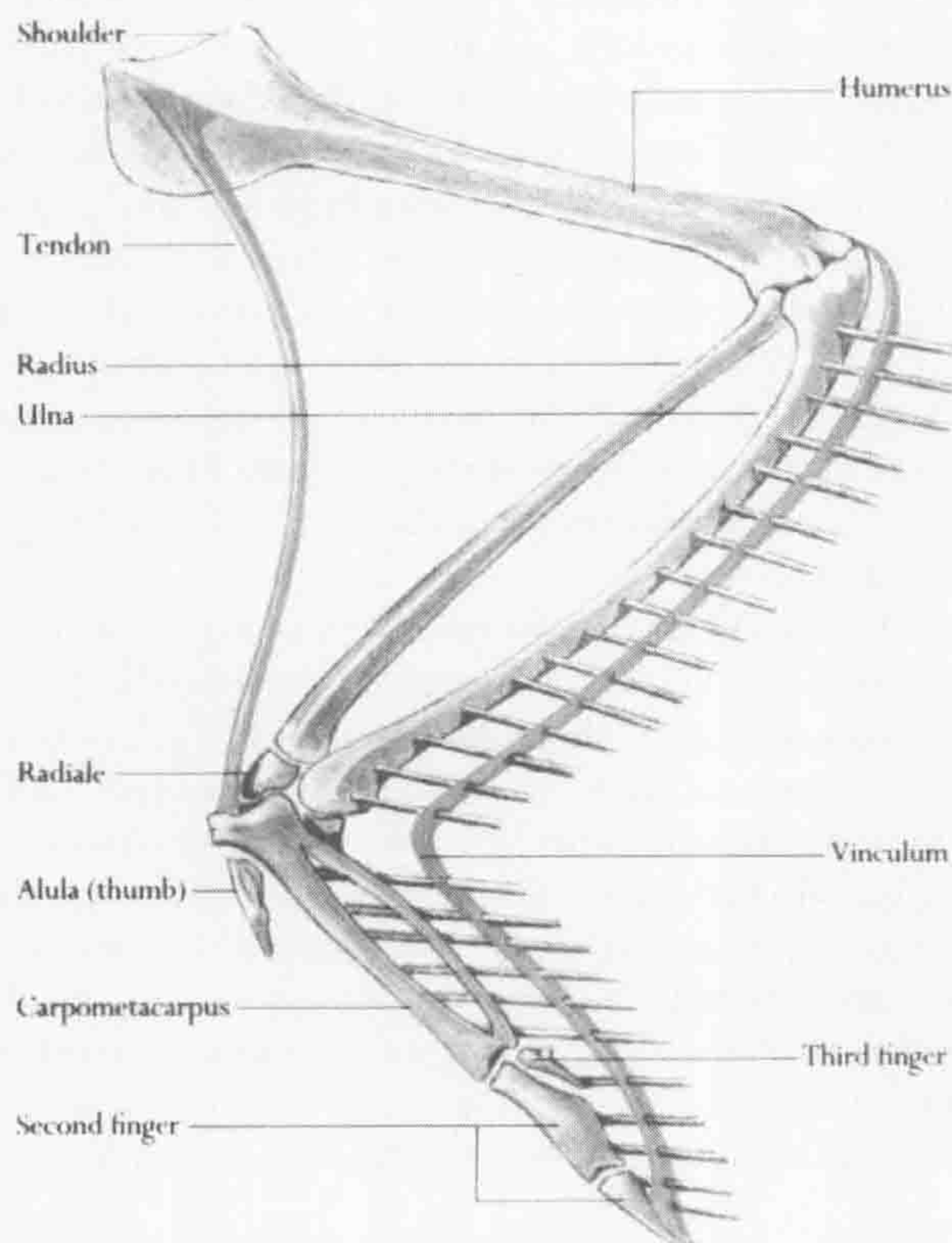
Reconstruction of *Archaeopteryx* skull by Paul Bühler, showing prokinesis, as in modern birds. The round dot marks the hypothetical craniofacial flexion zone, between the nasal and frontal bones, termed a nasofrontal hinge. The braincase is larger than it had been supposed, and Bühler's studies indicate that *Archaeopteryx* was much more bird-like than had been assumed previously, having among other avian features a prokinetic skull with an "inflated" and much more voluminous braincase. (From Bühler 1985; courtesy Academic Press.) Before Bühler's studies, the skull of *Archaeopteryx* was assumed to be of a reptilian, mesokinetic type, as in illustration at bottom, in which the hinge is between the parietal and frontal bones. It has been assumed that the modern prokinetic avian skull is derived from a reptilian mesokinetic type. (From Bock, *Journal of Morphology*, copyright © 1964; reprinted by permission of John Wiley and Sons.) Modern birds have evolved diverse forms of cranial kinesis, including rhynchokinesis (ratites and shorebirds) and amphikinesis (specialized shorebirds).

Schematic figures of a crow skull seen from the side (A), from beneath (B), and from the side with the mandible and the postorbital ligament in place (C), illustrating the movement of the upper jaw in cranial kinesis. The anterior and posterior movements of the various elements of the palate associated with the up and down movements of the upper jaw in prokinesis are shown in A and B. The positions of the open jaws (stippled) relative to the closed jaws are shown in C. (From Bock, *Journal of Morphology*, copyright © 1964; reprinted by permission of John Wiley and Sons)



Right ankle region of (left) young chicken (*Gallus*) and (right) mature chicken, showing contribution of the tarsals to the tibiotarsus and tarsometatarsus. Front view not to scale. Bird embryos have at least three tarsal elements, but their identities remain obscure (Holmgren 1953). (Modified after Bellairs and Jenkin 1960; courtesy Academic Press)

Homologies of the forelimbs and hindlimbs of a bird and a human. (From Van Tyne and Berger, *Fundamentals of ornithology*, copyright © 1976; reprinted by permission of John Wiley and Sons)



The main bones of the wing. The three avian metacarpals are fused to two carpals to form the avian carpometacarpus, the main bone of the avian hand. The two carpal elements, the ulnare and radiale, at the distal ends of the ulna and radius, respectively, lie between the forearm and manus and play an important role in supporting and controlling wing movements in active flapping flight. These carpal elements appear to restrict the movements of the manus and thus keep the primary feathers in proper alignment during the upstroke and downstroke (Vasquez 1992). The tendon running from the shoulder to the wrist stops the wing from opening too far and stretches the web of skin that forms the leading edge of the wing. A ligament, the vinculum, holds the flight feathers in place. (From Burton 1990; drawing by Sean Milne; courtesy Eddison Sadd Editions)